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# A NEW APTEROUS GENUS AND SPECIES OF ARADINAE FROM MEXICO (HEMIPTERA-HETEROPTERA, ARADIDAE)

*By* NICHOLAS A. KORMILEV

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# A NEW APTEROUS GENUS AND SPECIES OF ARADINAE FROM MEXICO (HEMIPTERA-HETEROPTERA, ARADIDAE)

*By* Nicholas A. Kormilev[1]

Abstract: A new genus (*Aradiolus*) and species (*A. paradoxus*) of flat bug belonging to the Aradinae is described from Mexico. The species represents the only apterous form known in the subfamily.

By the kind offices of Dr. Charles L. Hogue, Curator of Entomology at the Los Angeles County Museum of Natural History, I have had an opportunity to study a very interesting new apterous aradid from Mexico, for which I wish to express to him my sincere thanks.

This specimen represents a new genus belonging to the subfamily Aradinae, in which were previously known, besides macropterous, also brachypterous and stenopterous, but not apterous forms. In the new genus the head, antennae, tip of the abdomen, and the whole ventral surface of the body, are those of an *Aradus*, but the thorax is quite different, somewhat resmbling that of *Tretocoris* Usinger and Matsuda (1959), an apterous genus from New Zealand belonging to the subfamily Chinamyersinae.

## **Aradiolus,** new genus

*Description*:

*Head* longer than width across the eyes. Anterior process of the head, and antennal segments II and III, covered with dense, short, inclined, incrustated bristles, giving them a look of roughness. Similar, but shorter, bristles on antenniferous tubercles and vertex. Anterior process long and strong, slightly tapering toward the tip, reaching over the base of antennal segment II. Antenniferous tubercles acute, divergent, with a minute lateral tooth. Eyes globose, and slightly stalked, placed near the hind border of the head. Preocular teeth distinct, postocular rounded. Vertex raised in the middle anteriorly, elevation surrounded posteriorly by a semicircular depression. Antennae strong, less than twice as long as the head, and as thick as fore femora. Antennal segments I and IV the shortest and equal in length, II more than three times as long, and III more than twice as long as I. Rostrum placed far from the tip of anterior process; rostral atrium open; bucculae short, rounded, not contiguous anteriorly; rostral groove moderately deep, open posteriorly; rostrum thin, reaches to hind border of prosternum.

*Notum* partially, and dorsal surface of abdomen almost entirely, covered with dense, round scales.

*Pronotum* very short and wide. Collar indistinctly separated from the disc. Anterior angles produced into small, rectangular lobes. Lateral borders ex-

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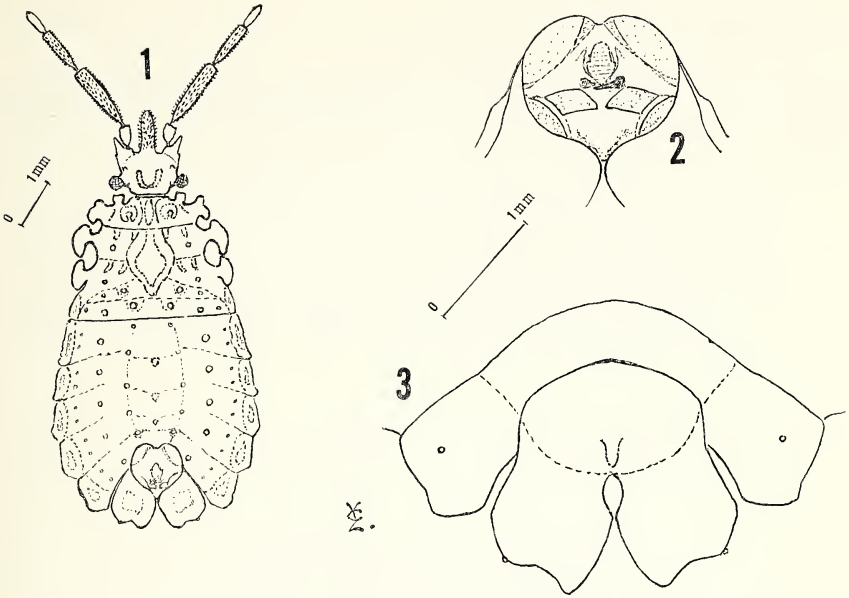


*Figures 1-3. Aradiolus paradoxus*, new genus and species. Fig. 1. dorsal aspect. Fig. 2. hypopygium, dorsal aspect. Fig. 3. sternum VII and genital cap, ventral aspect.

panded into two hammer-shaped lobes. Disc with two parallel carinae along median sulcus, and with two semicircular, black, opaque spots. Laterad of the latter are two fine longitudinal carinae.

*Mesonotum* separated from pronotum by a thin, but distinct sulcus. Middle of meso- and metanotum together occupied by a spear-shaped plate, depressed in the middle. Four small, black, opaque spots along fore border of mesonotum; two small, round, opaque spots behind outer of these. Lateral borders expanded into two "T"-shaped lobes.

*Metanotum* laterad of median plate separated from mesonotum by thin sulci; its oblique hind borders, laterad of median plate, semifused with tergum I. Lateral borders expanded into two "T"-shaped lobes. Disc with similar spots as mesonotum.

*Wings* completely absent.

*Abdomen* ovate, longer than maximal width across segment V. Tergum I separated from tergum II by a fine, transverse sulcus. Tergum II separated from central dorsal plate by a more distinct sulcus. Formula of round callous spots on terga, 2:1:1. Scars of dorsal scent gland openings situated between terga III, IV, V, and VI respectively. Connexival segments clearly separated from each other, but terga separated from each other only laterally, boundaries

absent mesally. Disc raised along median line, forming a wide, gently sloping ridge. Segment VIII in the male forming two large genital lobes, similar to *Aradus*. Hypopygium covered from ventral side by a semiglobose genital cap (segment IX), but open on dorsal side, as in *Aradus*. Exterior borders of connexiva II to IV straight, but angularly rounded on connexiva V to VII. Spiracles small, ventral, placed far from lateral, and nearer to fore border, on sterna II to VII; lateral and visible from above on genital lobes (VIII).

Ventral surface of the body similar to that of *Aradus*. Pro- and mesosternum deeply sulcate on median line for the reception of rostrum; metanotum and venter finely sulcate on median line.

Legs unarmed; trochanters completely fused with femora, the latter cylindrical; tibiae also cylindrical; fore tibiae near the apex interiorly with a minute tooth, or spine. Claws without arolia.

*Type species*: *Aradiolus paradoxus*, new species

In addition to the above description, further characters pertaining to the type specimen are as follows:

## **Aradiolus paradoxus**, new species

Figures 1 through 3

*Male*: Ovate, flat. Piceous; central meso-metanotal plate, bases of meso-metanotal lateral expansions, the whole abdomen from above, and the ventral surface of the body reddish brown, with exception of genital cap and hypopygium which are black; round callous spots on terga II to VII reddish. Tibiae with three black rings (basal, mesal, and apical).

*Measurements*: Head proportions 45:40 (= length:width of measured part); proportions of antennal segments, I to IV, are 11:37:24:11. Pronotum 17:62.5; mesonotum, with exception of meso metanotal median plate, which is 30 units long, 20:81; metanotum 10:84. Abdomen 120:104, at segment V.

Total length, 8.4 mm.; width of pronotum, 2.5 mm.; width of abdomen, 4.16 mm.

*Holotype*: Male, MEXICO, Oaxaca, 12 mi. so. of Chivela, A. S. Menke and L. A. Stange coll., VIII. 18, 1959. Deposited in the Los Angeles County Museum of Natural History.

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## NEW SPECIES OF NORTH AMERICAN *AMMOPHILA*, PART III. (HYMENOPTERA, SPHECIDAE)

*By* A. S. MENKE

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# NEW SPECIES OF NORTH AMERICAN *AMMOPHILA*, PART III.[1] (HYMENOPTERA, SPHECIDAE)[2]

*By* A. S. Menke[3]

Abstract: *Ammophila moenkopi* and *shoshone* are described from Arizona, and Wyoming and Utah, respectively. *Ammophila azteca* Cameron, new subspecies *clemente*, is described from San Clemente Island off the coast of southern California. These species belong in the *azteca* species group which is defined, and the included species are listed. New synonymy is given as follows: *azteca* Cameron, 1888 (= *pilosa* Fernald, 1934, *aculeata* Fernald, 1934), *peckhami* (Fernald), 1934 (= *willistoni* Fernald, 1934), *strenua* Cresson, 1865 (= *denningi* Murray, 1951), *varipes* Cresson, 1865 (= *comanche* Cameron, 1888).

Among material recently sent to me for identification by Mr. and Mrs. J. Davidson, Arizona State University, was a new species collected in northeast Arizona. This species, and another undescribed and related species from Wyoming and Utah are being described now so the names will be available to the Davidsons who are engaged in a study of *Ammophila* distribution in Arizona.

An undescribed subspecies of *Ammophila azteca* from one of the Channel Islands off the coast of southern California has been found in material sent to me by Dr. Fred S. Truxal of the Los Angeles County Museum of Natural History. This material was collected by the museum's Channel Island Biological Survey team in 1939. Additional specimens of this new subspecies were subsequently located in material on loan from Cornell University and the United States National Museum. I am describing this subspecies here because *azteca* is a close relative of the two new species. A more comprehensive treatment of these new taxa will be given when my revision is published.

Abbreviations used in citing type depositories are as follows: Arizona State University (ASU), Cornell University (CU), Los Angeles County Museum of Natural History (LACM), United States National Museum (USNM), University of California, Davis (UCD), California Academy of Sciences (CAS), and the Museum of Comparative Zoology, Harvard (MCZ).

The species described here belong to an assemblage I call the *azteca* group. All of the species in this group have a long preëpisternal sulcus; *e.g.*, it

[1]Parts I and II appeared in Acta Hymenopterologica 2:5-27 (1964) and Proc. Biol. Soc. Wash. 79:25-40 (1966).

[2]A biproduct of research supported by a Sigma Xi-R.E.S.A. Grant-in-Aid.

[3]Research Associate, Los Angeles County Museum of Natural History; Department of Entomology, University of California, Davis.

extends well below the pronotal lobe and ends in the sternal region. In those species of the group in which the sculpture of the mesopleuron is obscured by appressed hair one must either scrape away the hair to see the sulcus, or study the hair carefully to see if a vertical line is discernible. With proper lighting and body angle this is easy to do after a little practice. The male genitalia are diagnostic in only a few species of this group. The aedeagi of the two species described here are similar to figures 12 and 14 in Menke (1964).

The species assigned to this group are: *acuta* (Fernald), *azteca* Cameron (= *pilosa* Fernald,[4] *aculeata* Fernald[4]) *breviceps* Smith, *californica* Menke,

[4]New synonymy based on study of types.

*evansi* Menke, *harti* (Fernald), *karenae* Menke, *mediata* Cresson, *peckhami* (Fernald) (= *willistoni* Fernald[4]), *pruinosa* Cresson, *regina* Menke, *strenua* Cresson (= *denningi* Murray[4]) and *varipes* Cresson (= *comanche* Cameron[4]).

## **Ammophila moenkopi** Menke, new species

Figures 1 and 3

*Holotype male*: length 14 mm.

*Color*: Black; tegula and metapleural flange red; petiole tergite red laterally; gastral segments I-III red, tergite IV red laterobasally, sternite IV red; legs red except coxae, mid- and hindtrochanters and basal half of hind femur; wings clear, veins yellowish-red basally, brown apically.

*Vestiture*: Head and mesosoma (except propodeal enclosure) covered with long dense erect silver hair; frons, clypeus, and gena with dense appressed silver hair; pronotal collar and scutum sparsely covered with appressed silver hair (sculpture not obscured); pronotal lobe, thoracic pleura and propodeal side densely covered with appressed silver hair (sculpture obscured).

*Structure*: Labrum truncate but corners broadly rounded; clypeal surface broadly, evenly swollen, free margin arcuate in outline but with a broad, shallow median emargination; collar outline in lateral view as in Figure 3a; collar and scutum moderately macropunctate, interspaces shining although with microsculpture; scutellum sparsely punctate anteriorly, longitudinally ridged posteriorly; propodeal enclosure transversely ridged, interspaces not punctate; metapleural flange broadly lamellate, outer margin angulate, angle with a deep, narrow notch (Fig. 1); midtibia with one spur.

*Female*: Average length 15 mm, range: 11 to 18 mm.

*Color*: As in male except mandible red basally, clypeal margin frequently red, petiole sternite red, petiole tergite frequently all red, gaster red except for black spot on tergite V, legs red except for black coxae and sometimes black hind trochanter dorsally.

*Vestiture*: Same as male.

*Structure*: Labrum rounded, clypeal disk moderately bulging, very sparsely macropunctate, punctures confined mainly to lateral areas, median free

*Figures 1-2.* Metapleural flange—1, *Ammophila harti* and *moenkopi*; 2 a-c, *A. azteca*, showing variation of flange in this species. *Figures 3-5.* Lateral profile of the pronotum, a = male, b = female—3, *A. moenkopi*; 4, *A. harti*; 5, *A. shoshone*.

margin usually poorly defined because of weakly formed lateral tooth; inner orbits moderately converging below; collar outline as in Figure 3; midtibia usually with two spurs; mesosomal sculpture and other details as in male.

*Types*: Holotype male: 4.5 mi. E. Moenkopi, on *Poliomintha incana*, Coconino Co., Arizona, 14 June, 1966, J. M. Davidson and M. A. Cazier (ASU). Twenty-four male and sixty-nine female paratypes from the following Arizona localities: *Coconino Co.*: Moenkopi, 2 to 4.5 mi. E., 13-27 June, 1966, on *Poliomintha incana*, J. M. Davidson and M. A. Cazier (ASU, UCD, USNM, LACM, CAS, MCZ). *Navajo Co.*: Hotevilla, 7000′, 28 June, 1966, on *Poliomintha incana*, J. M. Davidson and M. A. Cazier (ASU, UCD); Jadito Trading Post, 28 June, 1966, on *Poliomintha incana*, J. M. Davidson, and M. A. Cazier (ASU).

*Discussion*: In some males the petiole sternite shows some reddening ventrally and gastral sternite IV is sometimes black. The apex of the hind tibia is occasionally blackish in both sexes. Although the base of the hind femur is black, the extreme base is reddish in nearly all the specimens studied. Out of

twenty-four males only three had two midtibial spurs, and in two of these cases one leg had only one spur. Occasional females have one spur on one leg and one specimen had only one spur on both midtibiae.

Except for the red legs and extensively red abdomen this species is similar to *harti* (Fernald) which has black legs, and which incidentally, was collected with *moenkopi* at its type locality on the same date. The form of the collar is also different in the two species. In *harti* it is somewhat longer in lateral profile, and more arcuate. In *moenkopi* the lateral profile is in the form of a gradual slope from the transverse line to the top of the collar. Thus, the top of the collar is narrower (from front to back) in *moenkopi* than in *harti* (compare Figs. 3 and 4). The clypeus of female *moenkopi* differs from *harti* in having much sparser punctation and a slightly duller surface. In *harti* the clypeus is rather evenly, moderately macropunctate and the surface is strongly shining. Besides *moenkopi* and *harti* the only other species in the *azteca* group that have a lamellate metapleural flange are *shoshone* n.sp. and *azteca* Cameron. The red legs and yellowish red color of the veins at the wing base easily separate *moenkopi* from both of these however.

## **Ammophila shoshone** Menke, new species
Figure 5

*Holotype male*: Length 15.5 mm.

*Color*: Black; tegula pale posteriorly; media and cubitus of forewing reddish brown basally, veins elsewhere brown; petiole tergite and gastral tergite I red laterally below spiracle, gastral sternite I red.

*Vestiture*: Head and mesosoma (except propodeal enclosure) with dense erect silver hair; frons, clypeus, and pronotal lobe with dense appressed silver hair; mesopleuron sparsely covered with appressed silver hair (sculpture visible) but denser along mesopleural suture forming a narrow band from midcoxa to bottom of hypoepimeral area; metapleuron and propodeal side sparsely covered with appressed silver hair (sculpture visible) but somewhat denser on inferior metapleural area near hindcoxa.

*Structure*: Labrum truncate but corner broadly rounded; clypeal surface broadly evenly swollen, free margin arcuate in outline but with a broad, shallow median emargination; collar outline in lateral view as in Figure 5a; collar and scutum moderately macropunctate, interspaces shining although with microsculpture; scutellum moderately punctate anteriorly, longitudinally ridged posteriorly; propodeal enclosure transversely ridged, interspaces not punctate; pleura and propodeal side moderately macropunctate, the punctures somewhat larger than on scutum; metapleural flange lamellate, angulate, the angle notched (similar to Fig. 1); midtibia with one spur.

*Female*: Average length 18 mm.

*Color*: Same as male except petiole tergite and gastral segment I red, II

red but tergite has an apical black spot (entirely red in Pilgrim Creek Camp female).

*Vestiture*: Essentially as in male except appressed silver hair of face sparser and sometimes lacking.

*Structure*: Clypeal disk moderately and evenly bulging, moderately macropunctate except anteromedially where punctures are sparser, median free margin scarcely defined because lateral tooth is very obtuse or absent; inner orbits moderately converging below; collar outline as in Figure 5b; midtibia with two spurs; other details as in male.

*Types*: Holotype male: Horse Creek Camp, Shoshone National Forest, Wyoming 21 July, 1957, A. and H. Dietrich (CU). Nine male and four female paratypes with same data as type (CU, UCD, LACM) and one female from Pilgrim Creek Camp, Grand Teton National Park, Wyoming, 27 July, 1957, A. and H. Dietrich (CU), and one male from Utah Lake, Utah, 1 August, 1933, G. P. Engelhardt (CU).

*Discussion*: The only appreciable variation among the males is the almost complete lack of red on the abdomen in one male, the more extensive reddening of gastral tergite I (red extends above spiracle) in three others, the presence of a trace of appressed silver hair on the gena in some others, and the presence of two midtibial spurs in six of the males (only on one leg in three of these).

This species is very similar to *A. harti* in every respect except color, scarcity of appressed silver hair, and the form of the pronotal collar. In lateral profile the collar is shorter in *shoshone* than in *harti* (compare Figs. 4 and 5). This seemingly slight difference is supported by the almost entirely black color of male *shoshone*. Color is very variable in *harti*, as would be expected in a species which has a broad geographical distribution (Arizona to Alberta and east to Quebec and North Carolina), but I have not seen a single male of *harti* in which melanism has reached the state found in *shoshone* males. Even the blackest males of *harti* have gastral tergite I completely red. The identification of females of *shoshone* and *harti* will be difficult since the only reliable means of separation is by the form of the collar and/or association with males. I have not seen any *harti* from the areas in which *shoshone* occurs, and this fact suggests that the latter may eventually prove to be a synonym. The red color and collar shape differences may only be the result of environmental influences, but a decision on this depends on the collection and study of more material from various Rocky Mountain area localities. However, I have seen one male of *harti* from 10 mi. N. Flowell, Millard Co., Utah (UCD) which is south of Utah Lake, a *shoshone* locality. This specimen is typical *harti*.

*Ammophila azteca* and *moenkopi* are the only other members of the *azteca* group with a lamellate metapleural flange. *Ammophila moenkopi* is easily separated from *shoshone* by its red legs. The separation from *azteca* may prove more difficult. *Ammophila azteca* is one of the most wide ranging species of the genus in North America being found from coast to coast although only in the northern states east of the Rockies. Its range extends north-

ward beyond the Arctic Circle in the Yukon Territory, and into Labrador in the east. Over this range it displays a perplexing array of variation in both color and sculpture. Some of these varieties mimic *shoshone* fairly well and they occur in the same area. This situation makes it difficult to separate the two species unless one has a thorough knowledge of *azteca*. The wing veins of *azteca* are uniformly brownish black and the scutal and pleural sculpture is rougher. The scutal punctation in *azteca* is usually denser than in *shoshone* and the interspaces tend to form wrinkles. The mesosoma of *azteca* is shorter in comparison with *shoshone* because in the latter the propodeum is more elongate. The metapleural flange is variable in *azteca* and it is often only narrowly lamellate or not lamellate (Fig. 2a-c). *A. azteca* males usually have two midtibial spurs. The median lobe of the clypeus is well defined in *azteca* females because of a strong lateral tooth.

### **Ammophila azteca clemente** Menke, new subspecies

This insular population is distinguished from typical *azteca* by color and vestiture. There are no structural differences.

*Diagnosis*: Black except for faint reddish tints on the petiole tergite laterally and on gastral segments I-II ventrally; wings lightly infumate; erect hair of head and mesosoma dirty white tending towards brownish dorsally; appressed silver hair found only on clypeus and frons of male, pronotal lobe, mesopleuron at midcoxa, and at side of petiole socket; face of female with sparse appressed brown hair, but sometimes with a trace of silver.

*Types*: Holotype male, San Clemente Island, Los Angeles Co., California, 3 April, 1939, collected by Los Angeles County Museum Channel Islands Biological Survey team (LACM). Seven male and seven female paratypes, all from San Clemente Island: 3-4, April, 1939, L.A. Co. Mus. Channel Island Biol. Surv. (LACM, UCD); 8-12 April, 1923, collector unknown (CU, UCD); May, 1939, J. T. Scott (USNM).

*Discussion*: The high degree of melanism in *clemente* is quite striking and easily sets this subspecies apart from the normally bicolored mainland *azteca*. In typical *azteca* males the petiole tergite and gastral segment I are red except for a narrow dorsal black stripe on each (sometimes the gastral tergite is completely red). In western *azteca* males the second, and sometimes the third, gastral segment may be largely red also. Females of typical *azteca* have the same amount of abdominal red but usually lack dorsal black markings.

The erect hair of mainland *azteca* is silvery rather than dirty white or brown and often the appressed silver hair is more extensive than in *clemente*. Females, for example, nearly always have much appressed silver hair on the frons and clypeus.

The metapleural flange in *clemente* is moderately lamellate in all specimens studied (Fig. 2b). In typical *azteca* it varies from broadly lamellate to not lamellate (Figs. 2a-c).

*Ammophila azteca* occurs on at least one of the other Channel Islands. I have seen one male (LACM) from Santa Rosa Island and interestingly it has the typical mainland color pattern and the erect hair is silver.

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1964. New species of North American *Ammophila*. (Hymenoptera, Sphecidae). Acta Hymenopterologica, 2(1): 5-27. (for 1963)

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LOS ANGELES COUNTY MUSEUM

# CONTRIBUTIONS IN SCIENCE

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# STUDIES ON CALIFORNIA ANTS. 3. THE TAXONOMIC STATUS OF *PROCERATIUM CALIFORNICUM* COOK (Hymenoptera: Formicidae)

*By* ROY R. SNELLING

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David K. Caldwell
*Editor*

# STUDIES ON CALIFORNIA ANTS. 3. THE TAXONOMIC STATUS OF *PROCERATIUM CALIFORNICUM* COOK (Hymenoptera: Formicidae)

*By* Roy R. Snelling[1]

Abstract: Based upon the type male, *Proceratium californicum* Cook is redescribed. The presumed females are described for the first time and the relationships to the species of the Old World and New World are discussed. A key to the workers and females of described New World *Proceratium* is provided.

In his book *The Ants of California,* Cook (1953) described several taxa as new. All of these, with the exception of *Proceratium californicum,* have since been synonymized with common, well-known species (Wilson, 1955; Cole, 1967). The identity of the *Proceratium* presented difficulties which, while not yet solved, can now be somewhat clarified.

## Historical Resume

As its name implies, this species was originally based on a specimen from California. Brown (1958) indicated caution in acceptance of this record, since there were no prior records of *Proceratium* in the United States from west of the Great Plains. The members of this genus are all cryptobiotic in their habitats and show a decided preference for areas which maintain high summer humidity. There are few areas in California which can satisfy this requirement; the type locality of *P. californicum* (the Santa Cruz Mountains) is one such area. On this basis, at least, it was not too unreasonable to expect a species of *Proceratium* to occur here.

The species was described from a single male specimen. Males of *Proceratium* are extremely rare in collections, and Cook's inadequate and inaccurate original description indicated no characters by which his species could be separated from the males of the eastern forms. The figures given by Cook are poorly executed, but at least offered clues lacking in the verbal description.

During recent years several alate females of a distinctive *Proceratium* have been taken in California, but it has not been possible to secure any workers or additional males. Nonetheless, for reasons which I hope to justify below, I believe these to be conspecific with *P. californicum.* Before going further into a discussion of these females it is pertinent to review the status of the male which Cook originally described.

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At the time Cook's publication appeared two similar and closely allied genera were recognized in the eastern United States, *Proceratium* and *Sysphincta*. For American workers, at least, the generic distinctions were obvious and clear-cut in the workers and females; M. R. Smith (1943) indicated equally sound characters for the males. In the latter caste, the main character used was wing venation. Not mentioned by Smith, but equally distinctive, is the clypeal configuration. In all castes of *Sysphincta* the clypeus possesses a distinct anterior median projection and the petiole is more or less nodiform (although this was recognized to be somewhat variable).

A cursory examination of Cook's figures show a distinctly projecting clypeal margin, a somewhat nodiform petiole and wing venation typically that of *Sysphincta*. Had any competent myrmecologist examined this specimen it would have been placed in that genus without hesitation. Cook was aware of Smith's work on male ants, having referred to it several times and taken a number of the illustrations directly from his paper, so it seems strange that he could have missed such obvious differences as were used to separate the two genera. Nowhere in his discussion of *Proceratium* does Cook make any mention of *Sysphincta;* neither did he attempt to compare his ant with any then placed in that genus.

Following a critical examination of nearly all the described species of *Proceratium* and *Sysphincta,* Brown (1958) found that the supposed generic differences would not hold up, as all the characters show graduation from the *Proceratium* extreme to the *Sysphincta* extreme. Accordingly Brown synonymized *Sysphincta* under *Proceratium*.

Attempts to recognize *P. californicum* from either Cook's description or figures prove futile. The textual comments are inaccurate and misleading and the figures bear little resemblance to the type specimen. The type, now the property of the Snow Museum, Oakland, California, has been made available to me, and with this specimen at hand, it is now possible to unravel some of the confusion and present a more detailed account of the species. Although I find it distasteful to review and criticize the original description in such detail as follows, I feel that if this is not done that there will remain the possibility of further confusion in the future.

## CRITIQUE OF COOK'S ORIGINAL DESCRIPTION AND A REDESCRIPTION OF *PROCERATIUM CALIFORNICUM*

Cook gave the length of the type specimen as 3.5 mm. I have carefully measured this individual, and arrive at a length of 4.25 mm; the distance from the anterior ocellus to the thoracic-petiolar articulation is 2.0 mm, the petiole measures 0.4 mm, and the abdomen (with apical segments reflected downward) is 1.85 mm. The statement that the head length (HL) is about equal to head width (HW) is correct; the HL is 0.82 mm, while HW is 0.84 mm, so that HW slightly exceeds HL. In specimens of *P. croceum* (Roger) HL is

0.60 mm and HW is 0.65 mm; according to Cook, the head of *P. californicum* is "broader than in *croceum*," while the above figures show the reverse to be true. Cook's next statement that the antennae are 12-segment is refuted by his figure of a 13-segmented antenna. Male ponerines typically possess 13-segmented antennae and there is no reason to suppose that *P. californicum* is an exception, particularly since the males of other *Proceratium*, so far as known, follow the rule. Unfortunately the type lacks the right funiculus and the entire left antenna. However, in the figure the funicular segments appear much too long (twice as long as broad), while typically they are hardly longer than broad in males of this genus. Since the facial view included only the right scape, the left antenna of the lateral view may be an illustrative addition to make the specimen complete. In the figure of the head the scape is shown distinctly longer than is actually the case. The statement that the scape is "equal in length to the last three segments of the funicle" can be neither proven nor disproven, although the figure shows the scape to be slightly longer; the scape is 0.42 mm long. The remaining cephalic features mentioned are correctly described, *i. e.*, the posterior margin of the head is rounded, three ocelli are present, the eyes are large and prominent, the well-developed mandibles are edentate with pointed apex. These characters are common to all *Proceratium* males. The eye length is 0.37 times HL and the distance from the lower eye margin to the mandibular insertion is about equal to one-third of the eye length (6:19); the upper eye margin is slightly below the midpoint of the HL.

The thorax is said to be short and massive. The thoracic length is 1.5 mm, maximum height is 1.2 mm and maximum width is 0.90 mm. I would not consider the thorax to be "short and massive" since the length exceeds both its height and width. Cook's statement that the pronotum has distinct humeral angles is baffling, for I cannot discern anything resembling humeral angles. The statement that the anteromedian part of the mesoscutum is distinctly truncated is also confusing. I assume that he had reference to the dorsal portion adjoining the promesonotal suture; this however is evenly convex. In spite of the claim that there is a large, rounded tubercule terminating centrally on the mesonotum, no such tubercle exists. Presumably this was in error for the metanotal tubercle, which is not large, and is rounded only in lateral aspect. From above it is pointed behind with a distinct median longitudinal carina.

The remaining gross characters are more or less correctly described, though without offering any distinctive features. In discussing the integument, his remark that most of the body is subopaque is not correct. Everywhere, except on the frons and epinotum, the surface is distinctly shining between the sculpturation. The cephalic sculpture is said to be fine, but the punctures are about equal to those of the thorax, where they are stated to be heavy and well-defined. On the frons and middle portions of the vertex the punctures are a little finer and much denser than elsewhere on the head; here the surface texture is roughened, but still there are sufficient shining raised interspaces that the aspect, on the whole, is that of a somewhat shining surface. The

punctures on the lower part of the face are irregularly linearly arranged, generally convergent toward the apex. The cheeks are crossed by a few very fine transverse striolae. The mandibles are shining, with numerous punctures a little larger than those of the adjacent portions of the face. The apical margin of the median clypeal lobe is acutely produced, with a pair of posteriorly convergent fine carinulae on its dorsal face.

The pronotum is reticulopunctate, with the surface distinctly shining and the punctures equal in size to those of the lower part of the frons. The mesopleurae are shining, with distinct punctures which are much denser below, especially anteriorly and posteriorly. The mesoscutum is densely punctate with distinct shining interspaces. The mesoscutellum is more strongly convex in lateral aspect than Cook's figure shows; the punctation is much like that of the mesoscutum. The epinotum is distinctly duller than the remainder of the thorax and is densely reticulopunctate. The figure of the petiolar node is inaccurate as it shows the anterior face more steeply sloping than is actually the case, and the node is too thick from front to back. The postpetiole is densely punctate, and the remaining gastric segments are a little shinier and more sparsely punctate.

The pubescence, both appressed and erect, is everywhere yellowish, not dark reddish-brown. The integument is dark reddish-brown. The wings are hyaline, very slightly whitish, with very pale yellowish veins and amber stigma. The hind wing has nine hamuli.

## The Type Specimen

The above commentary of conflicting statements was based upon the type specimen, the only known male of this species. Cook cited the data for this specimen as follows: "Glenwood in the Santa Cruz Mountains (T. W. Cook, 1950)," thus suggesting that he collected the specimen. In fact, the male bears the following data: "Glenwood Cal./27 May 1908." Dr. W. L. Brown has suggested (*in litt.*) that this specimen was "probably a Bradley-collected specimen from the MCZ." However, I have seen other insects with an identical label in the Stanford University collection, to which Cook had access. This male bears, in addition, two other penciled labels in Cook's handwriting. These read: "PROCERATIUM/sp./DRAWN" and "*Proceratium/californicum/* T. W. Cook/Described," indicating beyond any doubt that this is the type of *P. californicum.*

## Additional Material

I have before me four female *Proceratium* from three widely separated California localities. One female is from Yuba City, Sutter Co., 27 April 1965, collected by W. Wiard while sweeping mixed *Rumex* and *Avena* on a ditch levee. The second specimen was taken at Valle Vista, Oakland, Alameda Co., 21 April 1918, collector not indicated but probably J. C. Bradley. Two females are from the Santa Monica Mts., Los Angeles Co., 19 April 1959, collected by

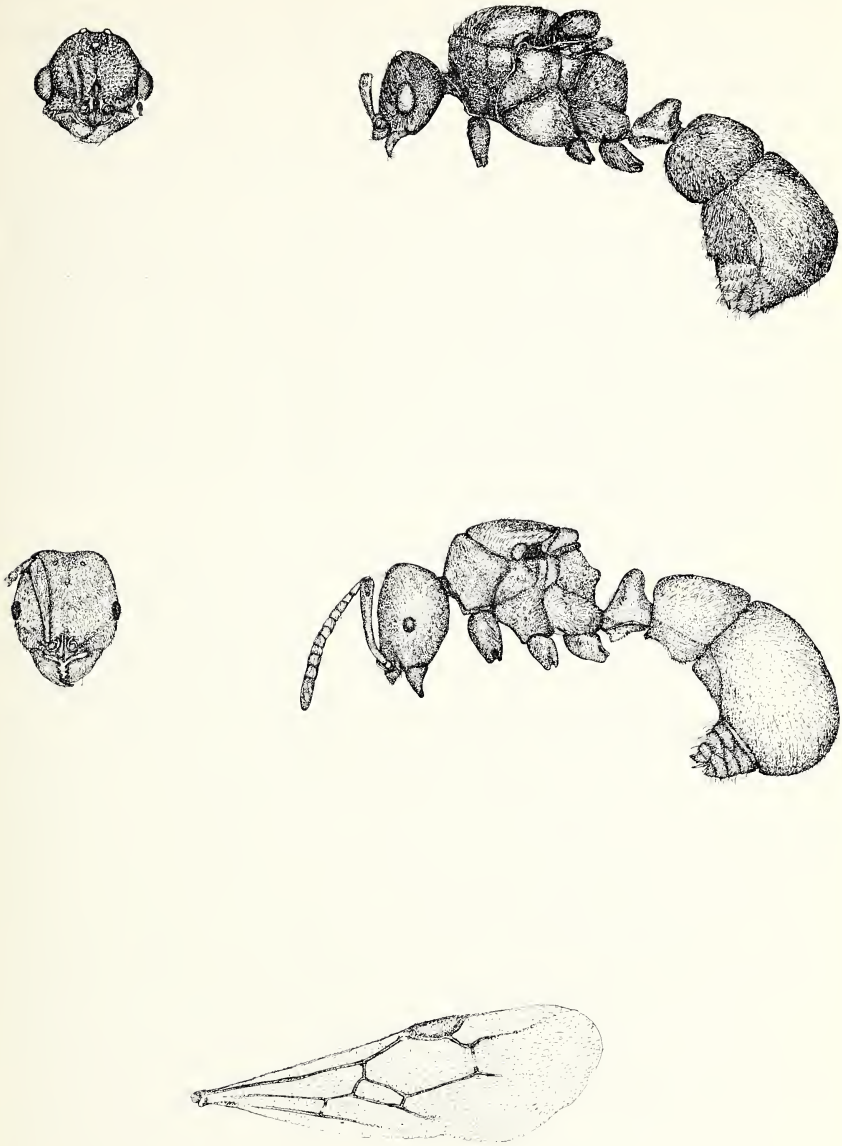

*Figure 1. Proceratium californicum* Cook. Frontal aspect of head and lateral aspect of body, respectively, of male Holotype (above) and female (middle); forewing (below).

an entomology student from the University of California at Los Angeles; according to Dr. J. N. Belkin the specimens were most likely taken at Tapia Park in Malibu Canyon. This park is a favored site for school field trips. Unfortunately, recent changes in the Tapia Park area have completely demolished the most likely sites.

All these females are conspecific; 15 years ago they would have been placed in the former genus *Sysphincta* with no difficulty. The clypeus is angularly produced in the middle, the petiole is somewhat nodiform in profile (though less so than is usual), the gastric configuration is more nearly that of *Sysphincta* than *Proceratium,* and the wing venation is typical of *Sysphincta.* As pointed out above, Cook erred in assigning his species to *Proceratium;* it should have, at that time, been placed in *Sysphincta,* with which it agreed in all essential characters. It was this realization, especially, which led me to assume that the females were also conspecific with Cook's species; both the male type and the alate females are typically *Sysphincta* in both habitus and structure and therefore readily separable from most of the Nearctic forms. In addition, there was the fact that no other members of this group had been previously discovered in California.

## COMPARATIVE NOTES ON *PROCERATIUM* SPECIES

Dr. Brown has very generously sent me specimens of a number of species of *Proceratium* for comparison with California material. The three eastern United States species, *P. croceum* (Roger), *P. pergandei* (Emery), and *P. silaceum* Roger, are represented in this material. From *P. croceum* and *P. silaceum,* the California females may be separated immediately by the produced clypeus and more nodiform scale. Both of the species lack any indication of an angular projection on the clypeal margin and the petiolar scale is fully erect and compressed from front to back so that it is much higher than long. The resemblance to *P. pergandei* is much closer, but fundamental differences are abundant. The paired carinae of the middle clypeal lobe of *P. pergandei* form a broad-based inverted "V" near the apex of the lobe which coalesce well below the level of the antennal sockets, the occipital margin is distinctly convex in full face view, the head, in full face view is not so markedly narrowed above the level of the eyes, the petiolar node is more depressed, the ventral petiolar projection is spine-like and directed caudad and the gastric configuration is quite distinct. In the females here associated with *P. californicum* the clypeal carinae form a much elongated inverted "V" and coalesce above the level of the lower margin of the antennal sockets, the head is markedly narrowed above the eyes, and the ventral petiolar process appears as a blunt, somewhat triangular lamella directed cephalad.

When compared with the Central American species, *P. micrommatum* (Roger), there are no obvious close relationships. In *P. micrommatum,* total length is much less, the antennal scapes are shorter and the petiolar and gastric configurations are different. Three of the Neotropical species, *P. convexiceps*

(Borgmeier), *P. mancum* Mann and *P. brasiliense* Borgmeier, are unknown to me except from their descriptions, which indicate, however, they are also quite distinct from the California form.

In short, *P. californicum* differs significantly from all its North American and Neotropical congeners and does not show any noteworthy affinity with any of these species.

In its general habitus it is obviously much more closely related to the Eurasian species, *P. melinum* (Roger), a member of the *melinum* group of Brown. This group includes also the Japanese species, *P. itoi* (Forel). Although the latter is not available, Dr. Brown sent me a female of *P. melinum* and comparison with that species is possible. When *P. californicum* and *P. melinum* are placed side by side, the similarity is striking; in size, color, punctation and configuration these ants are obviously very close. In *P. melinum* the occipital margin is evenly convex whereas in *P. californicum* the border is distinctly concave in the middle; the antennal scape is noticeably shorter in the Eurasian species, in full face view barely attaining the level of the hind margin of the posterior ocelli; in *P. californicum* the scape extends slightly above the level of the posterior ocelli. The frons is densely punctate, appearing granulose, and dull in *P. melinum;* in the case of *P. californicum* the punctures are finer, less distinct and the surface is slightly shining. Thoracic punctation offers an excellent character for separating the two species. Although it is consistently coarser and denser everywhere in *P. melinum,* the distinction is most marked on the mesoscutum. Here, in *P. melinum,* the punctures are very crowded, with the surface appearing subgranulose; the individual punctures are difficult to distinguish. The mesoscutal punctures of *P. californicum,* while abundant, are discretely separated by shining interstices. The second gastric segment of *P. melinum* is abundantly marked by distinct punctures which are only slightly finer than those of the mesoscutum, obviously much larger than the diameter of the hairs arising from them. The Nearctic species has a very finely punctate second gastric segment, the punctures only slightly larger in diameter than the hairs arising from them, much finer than the mesoscutal punctures. The petiolar process of *P. melinum,* in lateral view, has the surface between the anterior and posterior angles emarginate, so that two spines are formed, one directed obliquely cephalad and the other obliquely caudad. In *P. californicum* the process is not emarginate and the entire, somewhat triangular process, is obliquely directly cephalad.

The above comparative comments apply solely to the females. The rarity of males makes it difficult to relate the type specimen to the males of other species. The clypeal configuration, wing venation and shape of the petiolar node adequately separate *P. californicum* from *P. croceum* and *P. silaceum.* I have seen no males of *P. pergandei*; that caste was described by M. R. Smith (1928), but not in sufficient detail for adequate comparative remarks. The following comments are therefore tentative. The length of the male described by Smith is given as 3.6 mm so that it may be seen that the western species is

about 0.5 mm larger. In *P. pergandei* the head, "when measured from side to side thru the eyes," is said to be slightly broader than long; when measured in this manner, the head of the male of *P. californicum* is about 1.3 times as broad as long, which I would be inclined to call distinctly broader than long.

Smith's statement that the pronotum is "somewhat concealed by the mesonotum" would seem to imply that the latter overhangs the former; this condition is not true of *P. californicum*. In this species, the posterior face of the pronotum is vertical and is not overhung by the mesoscutum. The gaster of *P. pergandei* is described as smooth and shining; since Smith noted the presence of punctures elsewhere on the body and made no mention of gastric punctures, I assume he meant there were no evident punctures, although very fine, piligerous punctures must surely be present. The first gastric tergum of Cook's species is conspicuously and closely punctate; the second segment is likewise conspicuously punctate, but the punctures are notably sparser and somewhat finer than on the first segment.

Males of the European species, *P. melinum,* have not been available to me. Although this caste was described by Emery (1895), the description is not sufficiently detailed to be of much assistance here. The size of Emery's male and the mention of abdominal punctures may corroborate the relationship to *P. californicum* suggested by the females of these species.

The evidence examined above indicates that *P. californicum,* based on a male specimen, is distinct from previously described species of New World *Proceratium,* while there is some indication that it may be more nearly related to the European species, *P. melinum*. This accords with what is known of the presumed females of *P. californicum* which are clearly distinct from those of the other known species of the New World. It is on the basis of the relationships expressed above that I have associated these females with *P. californicum*.

The following key has been prepared to facilitate the identification of females and workers of the described species of *Proceratium* occurring in the New World. The following three species are placed in the key on the basis of comments in the literature as they have not been available to me: *P. brasiliense* Borgmeier, *P. convexiceps* (Borgmeier) and *P. mancum* Mann.

## KEY TO NEW WORLD *PROCERATIUM,* WORKERS AND FEMALES

1. Petiole erect, compressed from front to back; middle lobe of clypeus not produced forward as a triangular process; females with distinct thin, blade-like process on middle of metanotum and with strong longitudinal carina on apical one-half or more of scutellum.....2

   Petiole nodiform, anterior face convex or strongly inclined, not compressed (except in *P. californicum*); clypeus produced medially as a narrow triangular lobe (except in *P. convexiceps*); female without blade-like process on metanotum; longitudinal carina usually absent from scutellum, when present, very faint, limited to posterior one-fourth, or less, of the segment.....4

2. Larger species, 3.75 to 4 mm; petiolar node, in profile, thick, blunt above, base little thicker than crest; frons with longitudinal carina extending forward between frontal lobes to clypeal base; sides of thorax coarsely rugose (eastern U.S.) ..... *croceum* (Roger)
   Smaller species, 2.75 mm or less; petiolar node, in profile, slender, base distinctly thicker than crest; frons with longitudinal carina ending at midpoint, or less, of distance toward clypeal base; sides of thorax with a few irregular rugulae, but mostly smooth ..... 3
3. Epinotal spines distinct; genal area punctate, distinctly shining; dorsum of thorax without pronounced transverse rugulae behind (C. Amer., s. Mex) ..... *mancum* Mann
   Epinotum without distinct spines, but angulate laterally at juncture of basal and declivious faces; genal area strongly rugulose; dorsum of thorax with prominent transverse rugulae behind (eastern U.S.) ..... *silaceum* (Roger)
4. Small species, 3.5 mm or less; head broadest above, slightly but definitely narrowed toward mandibular insertions; frontal carinae approximate, subparallel (except in *P. brasiliense*) (Central and South America) ..... 5
   Larger species, 3.75 mm or more; head little, if any, narrowed toward mandibular insertions, broadest below level of eyes; frontal carinae well-separated, convergent above (U. S.) ..... 7
5. Clypeal margin not medially produced ..... *convexiceps* (Borgmeier)
   Clypeal margin slightly to strongly produced in middle ..... 6
6. Eyes very small; frontal carinae convergent anteriorly; ventral petiolar process bispinose ..... *brasiliense* Borgmeier
   Eyes larger, well-developed; frontal carinae parallel; ventral petiolar process with a single spine ..... *micrommatum* (Roger)
7. In full face view occipital margin convex, sides of head sub-parallel to top of head; clypeal carinae forming inverted broad-based "V" near apex; ventral petiolar process forming a narrow spine obliquely directed caudad; reflected dorsum of second gastric segment strongly projected to rear so that reflected tip of gaster appears to arise from mid-ventral surface ..... *pergandei* (Emery)
   In full face view occipital margin with median concavity, head distinctly narrowed above; clypeal carinae forming elongated inverted "V" before coalescing between frontal lobes; reflected dorsum of second gastric segment not strongly projecting to rear, forming an even curve with reflected tip ..... *californicum* Cook

During the preparation of this paper I have been supplied with material from several institutions. Especially helpful has been Dr. W. L. Brown, Jr., Cornell University, who sent specimens which would not have been otherwise available; Dr. Brown has also read and criticized the manuscript. The holotype of *P. californicum* was made available through the courtesy of Dr. C.

Don MacNeill, Snow Museum, Oakland, California. Dr. Marius Wasbauer sent the Yuba City specimen from the collection of the Bureau of Entomology, California Department of Agriculture. To these gentlemen, my very sincere thanks. To my wife, Ruth Ann, special thanks for the care and diligence with which she executed the habitus illustrations.

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# THE AMERICAN ATHERINID FISHES OF THE GENUS *COLEOTROPIS*

*By* CARTER R. GILBERT AND DAVID K. CALDWELL

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David K. Caldwell
*Editor*

# THE AMERICAN ATHERINID FISHES OF THE GENUS *COLEOTROPIS*

*By* Carter R. Gilbert[1] and David K. Caldwell[2]

Abstract: The atherinid fishes of the genus *Coleotropis* comprise two species, *C. starksi* (Meek and Hildebrand) and *C. blackburni* Schultz, which are found in shallow inshore waters of the eastern Pacific and western Atlantic oceans, respectively. A third species, *C. colecanos* Caldwell, recently described from Caribbean Costa Rica, is here synonymized with *C. blackburni*. The genus was included in the subfamily Menidiinae by Schultz (1948), who indicated that its closest relatives are the eastern Pacific genera *Eurystole* and *Nectarges*. The present paper describes the genus *Coleotropis* and its included forms, lists the morphological differences by which the species may be separated, and extends both the geographic ranges and ranges of morphometric variation of the two species.

## Introduction

The genus *Coleotropis* was erected by Myers and Wade (1942: 136-138) to include a single species, *C. starksi,* which had been described by Meek and Hildebrand (1923: 267, pl. 20, fig. 2) from Panama Bay. Later, Schultz (1949: 108-109, fig. 15) and Caldwell (1962) described, respectively, *C. blackburni* and *C. colecanos,* cognate forms from the Caribbean. The last species was described from a single specimen and was said to differ from *C. blackburni* in having a more slender body and a longer and more slender caudal peduncle. Although the morphometric data given in the original description of *C. colecanos* appeared convincing, the absence of any meristic features different from those found in *C. blackburni,* together with the scarcity of specimens, cast some doubt as to the validity of the species.

During the summer of 1963, intensive field work by the senior author in the vicinity of Tortuguero, Costa Rica (the type locality of *C. colecanos*), resulted in the collection of over a hundred specimens of *Coleotropis.* This large series has permitted a reassessment of the two Atlantic species, as well as a more detailed comparison of the Atlantic and Pacific forms.

## Materials and Acknowledgments

The specimens examined during this study are from the following museum collections: Field Museum of Natural History (formerly Chicago Natural History Museum) (FMNH); Florida State Museum, University of Florida (UF); Los Angeles County Museum of Natural History (LACM); Museum of Comparative Zoology, Harvard University (MCZ); University of

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California, Los Angeles (UCLA); University of Puerto Rico, Institute of Marine Biology, Mayaguez (UPR); and the United States National Museum (USNM). We wish to thank the individuals in charge of these collections, other than our own, for making the specimens available. We also want to express our appreciation to Dr. Archie F. Carr, of the University of Florida, whose generous help and financial support has resulted in many valuable fish collections from the Tortuguero area; to Dr. C. Richard Robins, Institute of Marine Science, University of Miami, and Mr. Alejandro Ciardelli, Universidad de Cartagena, Cartagena, Colombia (formerly of the Institute of Marine Science, University of Miami), for information regarding the hydrography of the Rio Atrato and Gulf of Urabá (Darien); to Mrs. Mildred Eaddy, Florida State Plant Board, who took the photographs; to Mr. Paul Laessle, University of Florida, for the illustrations; and to the authorities of the United States Fish and Wildlife Service Biological Laboratory, Brunswick, Georgia, and particularly to Mr. Herbert Gordy, who is responsible for the radiographs used in this study.

## METHODS

All counts and measurements included in this paper were taken by the senior author. These were made, using the standard methods described by Hubbs and Lagler (1958: 19-26), on the holotype and 21 topotypes of *Coleotropis colecanos* (ranging from 41.5 to 92 mm standard length) from Tortuguero, Costa Rica; on three paratypes and one non-type specimen of *C. blackburni* from Venezuela and Brazil, respectively; on six paratypes of *C. starksi* from Panama; and on 14 specimens of *C. starksi* from Costa Rica. Additional counts were made on a fourth paratype of *C. blackburni,* eleven other topotypes of *C. colecanos,* and ten other specimens of *C. starksi* from Costa Rica. Measurements are expressed in thousandths of standard length (shortened hereafter to SL); they were taken with precision dividers and were read to the nearest tenth of a millimeter. Scale counts for the circumferential and caudal-peduncle series are written to indicate the relative disposition of scales above and below the lateral line. Thus, a count expressed as 7-2-7=16 signifies seven scales above and seven scales below and between the lateral lines on each side of the body. The sum of these two counts, together with the lateral-line rows, represents the total count. Since the lateral line is incomplete and irregular, a lateral-scale count was obtained by counting the series from above the opercular opening to the caudal base. A frequency distribution expressed as (21) 23 to 25 (26) indicates that 90 percent of the counts fall between 23 and 25, with the extremes 21 and 26. The caudal fin-ray count is written so as to indicate the total number of caudal elements, as well as the number of main (long) caudal rays emanating from the superior and inferior hypurals. Thus, a count of 9+8=17 indicates nine dorsal and eight ventral main caudal rays. Vertebral counts are written so as to indicate the numbers of precaudal and caudal vertebrae, as well as the total number.

In this paper a complete description is presented under the account of the genus *Coleotropis;* no description appears in either of the species accounts. Characters distinguishing the two species are compared in the species diagnoses, and the rough breakdown of meristic counts also appears in these sections. The illustrations in Figures 2 through 5 were made from the specimens appearing in Figure 1.

## Genus *Coleotropis* Myers and Wade

*Menidia* Bonaparte, 1836: 91 (type species, *Atherina menidia* Linnaeus, by absolute tautonomy).

*Coleotropis* Myers and Wade, 1942: 136-138 (type species, *Menidia starksi,* by monotypy).

*Description:* Compressed, rather elongate atherinid fishes with the air bladder not tapering to a point posteriorly and not extending into five or more haemal arches; air bladder and posterior end of body cavity falling well short of anal fin origin; anal fin elongate, with a single spine; a sheath of scales present at base of anal fin, this sheath consisting of either one or two rows of scales anteriorly; body scales cycloid, the posterior edge somewhat irregular; origin of anal fin anterior to origin of first dorsal fin, midway between caudal base and posterior margin of orbit; dorsal fin widely separated, the height of the spinous portion less than distance between the origins of the spinous and soft-rayed segments; first dorsal fin with III or IV flexible spines, the origin over base of fourth or fifth anal ray; caudal fin forked; pectoral fin high on body, falcate, as long as or slightly longer than head, its tip extending beyond ventral base; pelvic fins posterior in position, close together and inserted equidistant between upper angle of pectoral base and anal origin; pelvic fins completely joined by a membrane; several enlarged scales present between bases of pelvic fins, the largest sharply pointed and extending posteriorly more than halfway along lengths of fins; anus normal in position, situated a short distance in front of anal fin.

Premaxillaries protractile, the dermal covering separated by a deep fold from skin on head; premaxillaries broadly dilated posteriorly, the anterior part not separated by a notch from the posterior part; gape of mouth strongly curved, restricted at corners by a membrane between the jaws; rami of mandibles scarcely elevated; teeth well developed in both jaws, sharply pointed, and slightly curved, in two rows, the first row in upper jaw enlarged; lower jaw slightly included at tip of mouth when mouth is tightly closed.

Abdomen more or less strongly compressed; peritoneum brownish-black; lateral line present, but irregular and incomplete; silvery lateral band present, very well marked, and sharply delimited above and below, somewhat constricted at caudal peduncle, and bordered above with a dark line.

Sides of head and body scaled; scales large, 38 to 50 in lateral series; predorsal scales 18 to 28; body circumferential scales 9-2-11 or 10-2-10 to 11-2-11=22 to 24; caudal-peduncle circumferential scales usually 5-2-5=12

or 7-2-7=16 (depending on species), with intermediate counts often present; anal rays I,19 to I,32; dorsal rays II-I to IV-I,7 to 10; pectoral rays 12 to 14, usually 13; pelvic rays I,5; gill rakers 4 to 6+1+14 to 17 (range of total counts=20 to 23); vertebrae 14 or 15+25 to 27 (range of total counts=40 to 42); total caudal rays 34, the main rays 9+8=17.

*Relationships:* Although the genotype of *Coleotropis, C. starksi,* was originally described in the genus *Menidia,* the relationships of the two genera actually are not particularly close. Myers and Wade (1942: 136-138), in the description of *Coleotropis,* made the following comments regarding the affinities of their new genus: "In Jordan and Hubbs' (1919) key, *Coleotropis starksi* keys down to the *Thyrina* group (*Thyrina, Thyrinops,* and *Atherinella*). It differs from all of these in its much larger size, the more curved gape, the considerably larger mouth (the maxillary reaching to below the front part of the eye), and very sharply in the deep anal sheath. None of the *Melaniris* (=*Thyrina,* preoccupied) group appears to possess any anal sheath at all. It may be remarked that *Melaniris brasiliensis* possesses neither the pinched belly nor the posteriorly produced air-bladder of the other species of *Melaniris,*[3] and it is a much larger fish. In these three characters *brasiliensis* resembles *starksi,* and it is possible that there is a close relationship. *M. brasiliensis,* however, has no anal sheath and possesses the small mouth of the other species of *Melaniris.* We therefore do not at this time disturb its generic assignment."

Schultz (1948) regarded the degree to which the air bladder extends into the haemal arches of the caudal vertebrae as particularly significant in atherinid classification. Using this criterion, he placed *Coleotropis* in the subfamily Menidiinae, the members of which have the air bladder not tapering to a point posteriorly and not extending beyond the fifth haemal arch. Inasmuch as Schultz made no direct statements regarding the inter-relationships of the various genera (the characters of the different groups appearing only in the form of a key), one must assume that he intended the proximity to each other of the couplets in the key to be a direct indication of phylogenetic relationships. According to this, *Coleotropis* is most closely related to the eastern Pacific genera *Eurystole* and *Nectarges,* and somewhat more distantly allied to *Adenops, Membras,* and *Hubbesia.* All of these taxons are characterized by having the posterior tip of the air bladder falling well short of the anal-fin origin.

*Ecology:* All specimens of *Coleotropis blackburni* from Tortuguero, Costa Rica, were collected in the surge zone area, in water from one to 36 inches deep. None was ever taken in brackish or fresh water, and thus they were never found sympatrically with *Thyrinops chagresi* (Meek and Hildebrand), the other atherinid fish in the Tortuguero area.

[3]According to Schultz (1948), the genus *Melaniris* does *not* have a pronounced posterior extension of the air bladder. He also erected a new genus, *Xenomelaniris,* for the sole reception of *"M." brasiliensis.*

Data for the most recent collections of *C. starksi* (from Costa Rica) indicate that this species occurs in ecological situations very similar or identical to those in which *C. blackburni* is found.

*Range:* (See under species accounts).

*Coleotropis starksi* (Meek and Hildebrand)
Figures 1A, 2A, 3A, 4A, 5A

*Menidia starksi* Meek and Hildebrand, 1923: 267-268, pl. XX, fig. 2 (original description; type locality, Taboga Island, Panama; holotype, 109 mm SL [incorrectly listed in original description as 235 mm SL], USNM 79732).

*Coleotropis starksi,* Myers and Wade, 1942: 136-138 (new generic name).

*Specimens Examined* (numbers in parentheses refer to number of specimens examined and size range in mm, respectively): FMNH 8308 (2 paratypes of *Menidia starksi,* 74-93.5), USNM 79733 (3 paratypes, 89-111), USNM 81747 (1 paratype, 111), all from Taboga Island, Panama; UCLA W 53-283 (26, 15-95), Isla de San Jose, Ensenada Playa Grande, Islas Perlas, Panama Bay, Panama; UCLA, W 54-168 (1, 43), Bahia Ballena, Golfo de

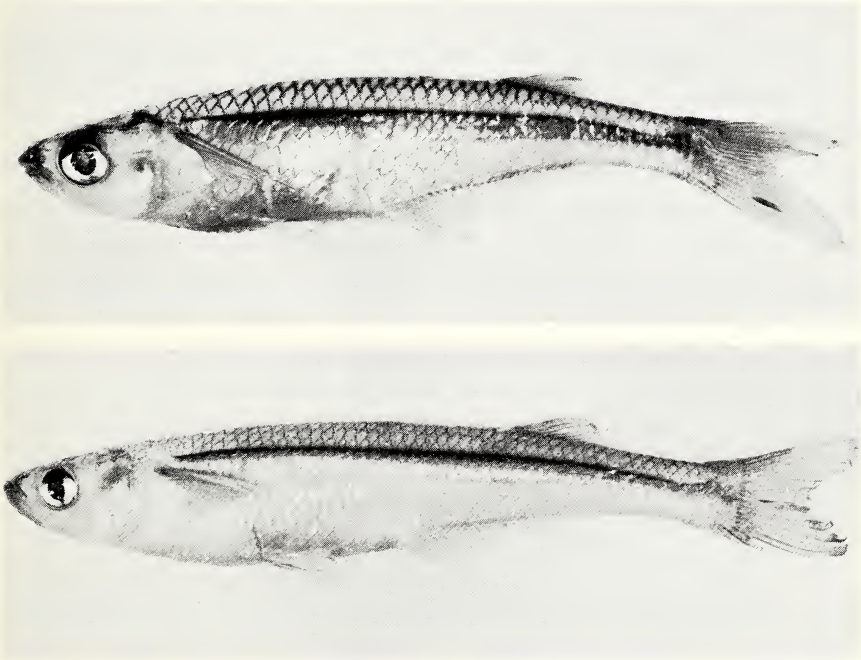

*Figure 1.* A: *Coleotropis starksi* (Meek and Hildebrand), LACM 6893-1, 90.5 mm SL, from Playa del Coco, near Sardinal, Costa Rica. B: *Coleotropis blackburni* Schultz, UF 11205, 90.5 mm SL, from Tortuguero, Costa Rica.

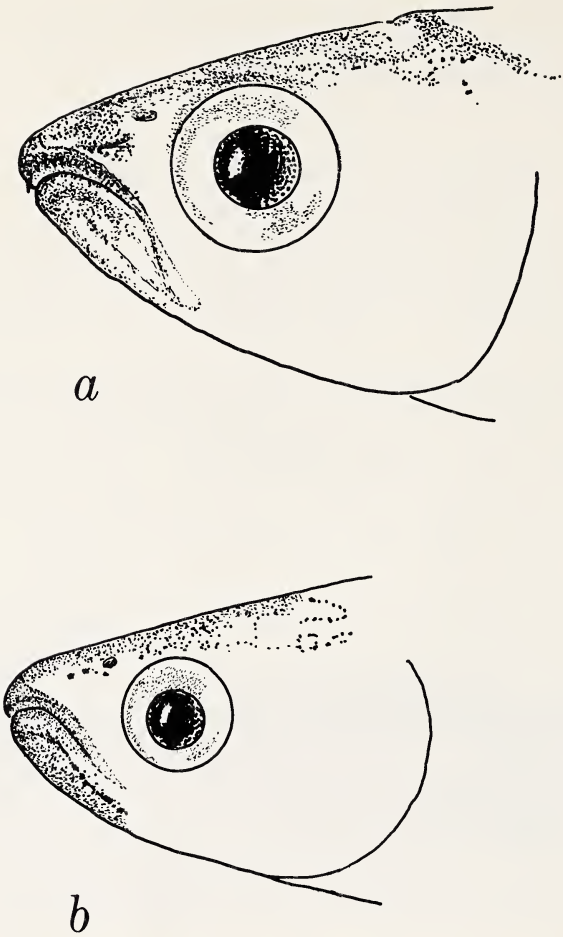


*Figure 2.* Comparison of mouth size in the two species of *Coleotropis.* A: *C. starksi.* B: *C. blackburni.*

Nicoya, Costa Rica; UCLA, W 54-172 (34, 31-99), UCLA, W 54-177 (24, 44-59), Isla Tortuga, Golfo de Nicoya, Costa Rica; LACM 6894-1 (2, 19-55), ½ mile south of Playa del Coco, near Sardinal, Costa Rica; LACM 6893-1 (22, 53-102), Playa del Coco, near Sardinal, Costa Rica.

*Diagnosis:* Characters mentioned in the generic description are not repeated here, except where greater clarification is required. Additional meristic data appear in Tables 1 through 5.

A species of *Coleotropis* that differs from its Atlantic cognate, *C. blackburni,* in having fewer predorsal scales (18 or 19 vs. 23 to 28); fewer lateral scales (37 to 39 vs. 43 to 50); fewer caudal-peduncle scales (usually 12 vs.

usually 16); fewer scales in circumferential series above and between lateral lines (9 vs. 10 or 11); a higher average anal fin-ray count (25 to 33 vs. 20 to 26); a larger mouth, the maxillary extending posteriorly to beneath anterior part of orbit (instead of extending just anterior to orbit) (Fig. 2A); an anal sheath with two scale rows anteriorly (instead of one) (Fig. 3A); a longer pectoral fin, which is slightly longer than head and extends to above tip of pelvic fin (instead of being shorter than head and extending about halfway along length of pelvic fin); the upper margin of silvery lateral stripe on third (rather than fourth) scale row below mid-dorsal scale row (Fig. 4A); pigmentation less extensive on lower jaw, covering less than half (instead of all) of jaw (Fig. 5A); teeth in both jaws larger and more widely spaced; a probable greater maximum body length (largest specimen [of 115] examined, 111 mm SL vs. 92 mm SL [124 specimens]).

Lateral scales 37 or 38 (39) (a count of 40 listed in original description); dorsal-fin rays (II) III (IV), (7) 8 (9); total anal elements (25) 26 to 29 (30 and 33); circumferential scales (9-2-9 or 8-2-11=20 or 21) 9-2-10 or 9-2-11=21 or 22 (9-2-12=23); caudal-peduncle scales 5-2-5=12; vertebrae (14+25=39) 15+25=40 (16+25=41).

*Range:* Recorded from the Gulf of Panama to northern Costa Rica. Further collecting undoubtedly will extend the range of this species.

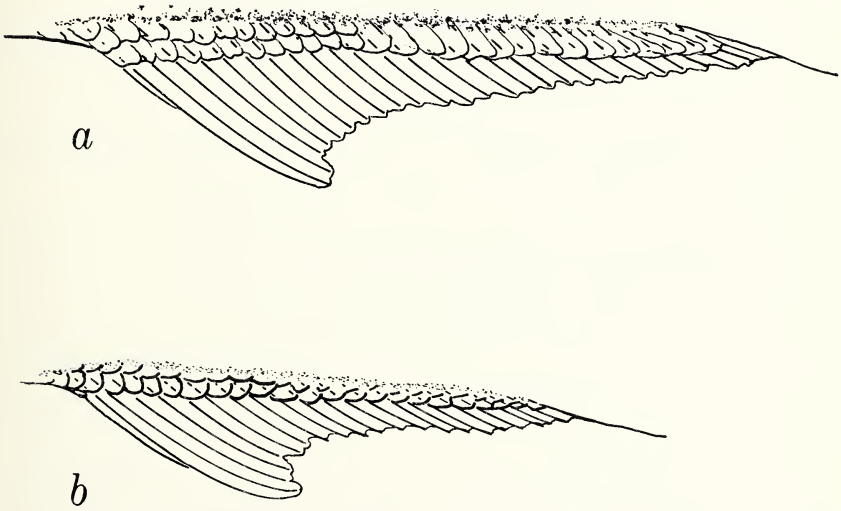


*Figure 3.* Comparison of anal sheaths in the two species of *Coleotropis*. A: *C. starksi*. B: *C. blackburni*.

*Coleotropis blackburni* Schultz
Figures 1B, 2B, 3B, 4B, 5B

*Coleotropis blackburni* Schultz, 1949: 108-109, fig. 15 (original description;

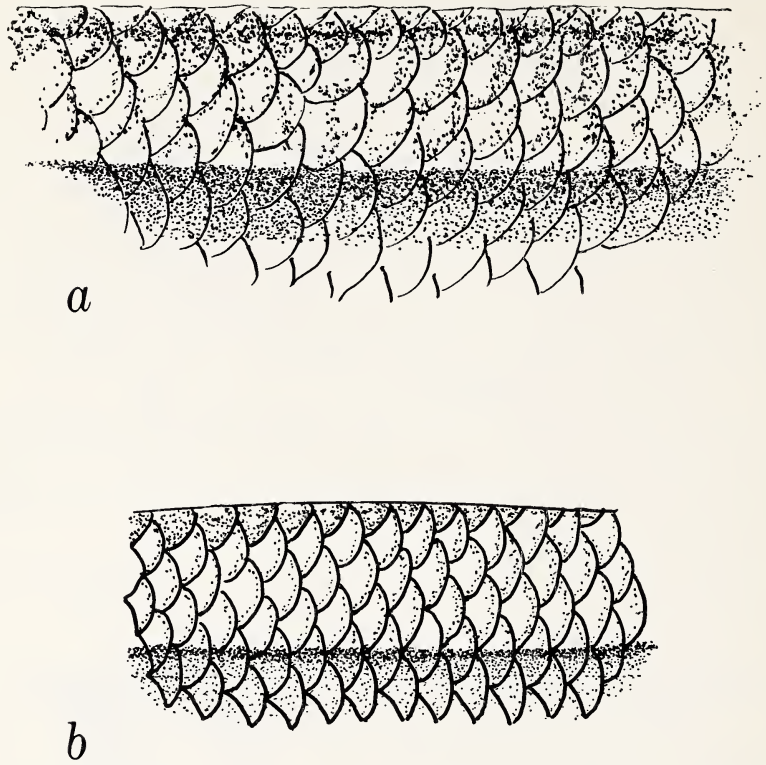


*Figure 4.* Comparison of scale size and position of lateral stripe on upper part of back in the two species of *Coleotropis*. A: *C. starksi*. B: *C. blackburni*.

compared with *C. starksi*; type locality, Jacuque Point, Gulf of Venezuela, Venezuela; holotype, 82 mm SL, USNM 123205).

*Coleotropis* sp., Caldwell, Ogren, and Giovannoli, 1959: 19-22, fig. 2 (one specimen from Tortuguero, Costa Rica; compared with *C. blackburni*).

*Coleotropis colecanos* Caldwell, 1962: 1-8, fig. 1-2 (original description; differs from *C. blackburni* in certain body proportions; type locality, Tortuguero, Costa Rica; holotype, 76 mm SL, UF 5652).

*Specimens Examined* (numbers in parentheses refer to number of specimens examined and size range in mm, respectively): USNM 123207 (3 paratypes of *C. blackburni*, 45-64), MCZ 37293 (1 paratype of *C. blackburni*, 48), all from Point Macolla, Gulf of Venezuela, Venezuela; UPR 2490 (3, 35-65), Manzanilla, Isla Margarita, Venezuela; USNM 100830 (1, 72), Porto Inhauma, Brazil; UF 5652 (holotype of *C. colecanos*, 76), beach near Tortuguero, Limon Province, Costa Rica; UF 11205 (84 topotypes of *C. colecanos*, 19-90.5), LACM 8335 (10 topotypes of *C. colecanos*, 37-61.5), shore in front of turtle camp, ca. 2 mi. S of mouth of Tortuguero lagoon, Limon

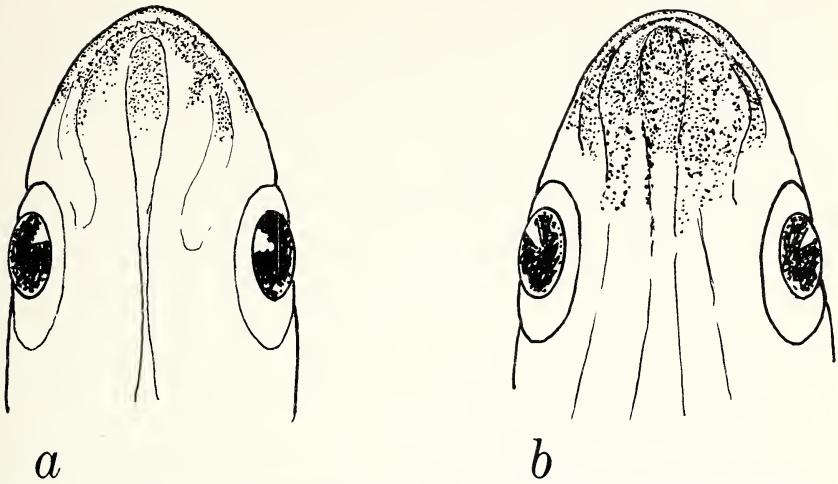


*Figure 5.* Comparison of pigmentation on underside of head in the two species of *Coleotropis.* A: *C. starksi.* B: *C. blackburni.*

Province, Costa Rica; UF 11254 (1 topotype of *C. colecanos*, 68.5), mouth of Tortuguero lagoon, Limon Province, Costa Rica; UF 11261 (23 topotypes of *C. colecanos*, 31-65), seaward side of sand spit, near mouth of Tortuguero lagoon, Limon Province, Costa Rica.

*Diagnosis:* Characters mentioned in the generic description are not repeated here, except where greater clarification is required. Additional meristic data appear in Tables 1 through 5.

A species of *Coleotropis* that differs from its Pacific cognate, *C. starksi*, in having more predorsal scales (23 to 28 vs. 18 or 19); more lateral scales (43 to 50 vs. 37 to 39); more caudal-peduncle scales (usually 16 vs. usually 12); more scales in circumferential series above and between lateral lines (10 or 11 vs. 9); a lower average anal fin-ray count (20 to 26 vs. 25 to 33); a smaller mouth, the maxillary extending to just in front of orbit (instead of to beneath anterior part of orbit) (Fig. 2B); anal sheath with one scale row anteriorly (instead of two) (Fig. 3B); a shorter pectoral fin, which is shorter than head and extends about halfway along length of pelvic fin (instead of being slightly longer than head and extending to above tip of pelvic fin); the upper margin of silvery lateral stripe on fourth (rather than third) scale row below mid-dorsal scale row (Fig. 4B); pigmentation more extensive on lower jaw, covering nearly all (instead of less than half) of jaw (Fig. 5B); teeth in both jaws smaller and more narrowly spaced; a probable smaller maximum body length (largest specimen [of 124] examined, 92 mm SL vs. 111 mm SL [115 specimens]).

Lateral scales (43) 44 to 49 (50); dorsal-fin rays III (IV), (7) 8 (9 or 10); total anal elements (20) 21 to 24 (25 or 26); circumferential scales

(10-2-10 or 11-2-9=22) 11-2-10 or 11-2-11=23 or 24 (11-2-12=25); caudal-peduncle scales (6-2-6 or 7-2-6=14 or 15) 7-2-7=16; vertebrae (14+26=40, 15+25=40, or 14+27=41) 15+26=41 (15+27=42).

*Range:* Known from the Caribbean coasts of Costa Rica and Venezuela eastward to the Atlantic coast of central Brazil. Additional collecting probably will extend the range of this species.

*Status of COLEOTROPIS COLECANOS:* In the preceding text only one species of *Coleotropis* (*C. blackburni*) from the western Atlantic-Caribbean area has been recognized, despite the fact that a second form (*C. colecanos*) was recently described by Caldwell (1962) from the Caribbean coast of Costa Rica. The reasons for this are discussed herein.

*Coleotropis colecanos* was described as differing from *C. blackburni* in having a longer and more shallow caudal peduncle and a lesser body depth. No meristic differences were noted.

Measurements and counts were made (by Gilbert) on four paratypes of *C. blackburni* from Venezuela, a non-type specimen from Brazil, and 25 topotypes of *C. colecanos*. In addition, the holotype of *C. colecanos* was recounted and remeasured. These data are summarized in Tables 1 through 5.

The new value obtained for the caudal peduncle depth of the holotype of *C. colecanos* agrees closely with the original (88 versus 84). The new value for the caudal-peduncle length is somewhat less than that given in the original description (205 versus 236). This undoubtedly is attributable to a slight difference in measuring technique. Nevertheless, this new value is greater than for all but seven (out of 38) of the topotypes measured, and is also higher than any of the values obtained for the four specimens from Venezuela and Brazil (Table 5). As can be seen from Table 5, the overall average for caudal-peduncle length is slightly higher for the topotypes of *C. colecanos* than for the paratypes and non-type specimen of *C. blackburni*. However, the fact that values obtained for *C. colecanos* completely encompass those for *C. blackburni* indicates that these differences are not meaningful. Since there apparently are no striking morphological differences by which *C. colecanos* and *C. blackburni* can be distinguished, we conclude that *C. colecanos* should henceforth be regarded as a synonym of *C. blackburni*.

Although the populations of *Coleotropis blackburni* from the extreme western Caribbean and from the southern Caribbean-western Atlantic apparently are indistinguishable, it should be noted that differences do exist between other elements of the inshore fish faunas occurring in these two areas. For example, in the southern and western Caribbean the sciaenid fish *Umbrina broussonnetii* is found only from western Colombia northward along the Central American coast, whereas the closely related *U. coroides* is confined almost exclusively to the South American coast. In the northern Caribbean these two species occur sympatrically (Gilbert, 1966). Another sciaenid, *Ophioscion costaricensis*, which is known from two specimens from the Tortuguero area, was said to differ from the closely related *O. brasiliensis*

(from the southern Caribbean and southwestern Atlantic) in having a significantly smaller eye and wider interorbital space (Caldwell, 1958). Examination (by Gilbert) of many additional specimens of *O. brasiliensis* confirms these differences.

The above faunal break seems to center around the Gulf of Urabá (Darien), which marks the boundary between South and Central America. Recent exploration by the *R/V Pillsbury* (of the Institute of Marine Science, University of Miami) in this area has resulted in ecological information pertinent to this problem. The following are preliminary observations, and thus may be subject to some modification when the data are analyzed in more detail (C. R. Robins, *pers. comm.*).

The Gulf of Urabá is a long, relatively narrow arm of the sea, which appears to be of nearly uniform depth throughout (ca. 20 fathoms). The bottom is uniformly flat except near shore, where the sides slope very sharply upward. The large quantities of silt that are carried in by the Rio Atrato are mostly deposited along the eastern shore of the Gulf or along the adjacent Caribbean coast of South America. This easterly flow is thought to be due to the Corollis effect and/or perhaps an eastward flowing oceanic countercurrent. The resultant ecological conditions favor such fishes as sciaenids and clupeids, most species of which characteristically inhabit shallow, turbid, inshore water where a silt bottom is present. In contrast, the western shore of the Gulf of Urabá, as well as much of the Caribbean coast of Panama, is largely silt-free, is characterized by extensive areas of small coral formations, and has a fish fauna that is basically an impoverished insular reef type. Such an area is poorly suited for most sciaenids and clupeids, and the species of these families collected to the east were not encountered here. Farther west one again finds ecological conditions similar to those on the coast of northern South America, and it is here that sciaenids and clupeids again appear. Thus, the distributional break noted for the sciaenid genera *Ophioscion* and *Umbrina* appears real, and might logically be expected in other groups of fishes.

TABLE 1

Predorsal scale counts in the two species of *Coleotropis*

| | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | No. | x |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. starksi* | 15 | 13 | | | | | | | | | | 28 | 18.5 |
| *C. blackburni*** | | | | | | | 2 | 3 | | | | 5 | 24.6 |
| *C. blackburni**** | | | | | | 2 | 3* | 4 | 8 | 13 | 3 | 33 | 26.1 |

*Value for holotype of *C. colecanos*
**Non-topotypes of *C. colecanos*
***Topotypes of *C. colecanos*

TABLE 2

Lateral scale counts in the two species of *Coleotropis*

| | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | No. | x |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. starksi* | 9 | 17 | 2 | | | | | | | | | | | | 28 | 37.8 |
| *C. blackburni*** | | | | | | | | 3 | 2 | | | | | | 5 | 44.4 |
| *C. blackburni**** | | | | | | | 1 | 7 | 3 | 8* | 4 | 5 | 3 | 2 | 33 | 46.3 |

*Value for holotype of *C. colecanos*
**Non-topotypes of *C. colecanos*
***Topotypes of *C. colecanos*

TABLE 3

Anal ray counts in the two species of *Coleotropis*****

| | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | No. | x |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. starksi* | | | | | | 1 | 8 | 4 | 9 | 6 | 1 | | | 1 | 30 | 27.7 |
| *C. blackburni*** | | | 2 | 2 | | | | | | | | | | | 4 | 22.5 |
| *C. blackburni**** | 2 | 3 | 5* | 13 | 7 | 1 | 2 | | | | | | | | 33 | 22.9 |

*Value for holotype of *C. colecanos*

**Non-topotypes of *C. colecanos*

***Topotypes of *C. colecanos*

****Includes the single anal spine plus the remaining soft elements

TABLE 4

Total vertebrae counts in the two species of *Coleotropis*

| | 39 | 40 | 41 | 42 | No. | x |
|---|---|---|---|---|---|---|
| *C. starksi* | 1 | 9 | 1 | | 11 | 40.0 |
| *C. blackburni** | | 1 | 3 | | 4 | 40.8 |
| *C. blackburni*** | | 4 | 14 | 1 | 19 | 40.8 |

*Non-topotypes of *C. colecanos*

**Topotypes of *C. colecanos*

TABLE 5

Comparison of proportional measurements (expressed in thousandths of standard length) in the species of *Coleotropis*

| | *C. starksi* | *C. starksi* | *C. blackburni** | *C. blackburni** | *C. blackburni*** | *C. blackburni*** | *C. blackburni**** |
|---|---|---|---|---|---|---|---|
| Size range in mm | 56.7-64.5 | 67.5-111 | 54-64 | 72 | 41.5-63 | 65-92 | 74 |
| No. of specimens | 6 | 14 | 3 | 1 | 18**** | 3 | 1 |
| Body depth | 183-205 (193.0) | 196-230 (215.6) | 200-207 (203.3) | 167 | 163-189 (176.8) | 172-194 (181.3) | 169 |
| Caudal-peduncle depth | 81-87 (84.0) | 83-101 (92.1) | 102-103 (102.3) | 103 | 92-104 (97.0) | 87-93 (90.7) | 88 |
| Caudal-peduncle length | 155-175 (165.5) | 135-178 (156.9) | 173-191 (182.0) | 188 | 169-224 (195.6) | 178-192 (185.0) | 205 |
| Head depth | 162-174 (169.2) | 158-180 (166.5) | 142-163 (152.7) | 136 | 139-159 (144.8) | 132-147 (139.7) | 138 |
| Head width | 118-131 (126.5) | 114-143 (126.1) | 104-116 (108.7) | 97 | 102-124 (111.2) | 99-104 (102.3) | 104 |
| Head length | 243-251 (246.7) | 221-258 (238.1) | 213-220 (216.7) | 213 | 198-239 (215.1) | 208-213 (211.0) | 213 |
| Length of lower jaw | 98-113 (107.5) | 94-114 (104.4) | 81-96 (89.7) | 76 | 76-93 (83.1) | 76-85 (80.0) | 78 |
| Snout length | 62-75 (67.0) | 68-82 (75.1) | 66-67 (66.3) | 63 | 60-92 (64.7) | 58-70 (63.0) | 68 |

TABLE 5 (CONT.)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Post-orbital length | 84-96 (89.4) | 81-96 (88.4) | 88-92 (89.7) | 88 | 84-92 (87.0) | 83-93 (88.3) | 88 |
| Orbital diameter | 79-95 (87.5) | 68-86 (76.8) | 64-69 (66.7) | 63 | 65-76 (70.4) | 57 (57.0) | 59 |
| Interorbital width | 72-79 (75.8) | 77-87 (81.5) | 69-78 (74.7) | 67 | 67-78 (72.0) | 65-73 (68.3) | 65 |
| Snout to 1st dorsal origin | 524-561 (541.7) | 536-611 (585.4) | 550-594 (569.3) | 553 | 532-609 (548.9) | 539-570 (553.6) | 547 |
| Snout to pelvic insertion | 344-380 (357.7) | 350-405 (380.3) | 344-363 (356.6) | 351 | 337-380 (351.1) | 348-376 (359.0) | 362 |
| Snout to anal origin | 495-529 (510.0) | 503-566 (539.9) | 488-523 (507.3) | 521 | 470-552 (498.6) | 494-540 (514.0) | 507 |
| 1st dorsal origin to 2nd dorsal origin | 126-154 (134.7) | 117-149 (132.0) | 118-141 (126.7) | 160 | 130-163 (144.5) | 139-160 (150.7) | 132 |
| Anal fin length | 357-405 (384.8) | 336-407 (369.4) | 308-341 (322.3) | 326 | 326-380 (343.9) | 302-349 (329.0) | 320 |

*Non-topotypes of *C. colecanos*

**Topotypes of *C. colecanos*

***Holotype of *C. colecanos*

****Caudal-peduncle length was measured for 35 topotypes under 65 mm SL

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LOS ANGELES COUNTY MUSEUM

# CONTRIBUTIONS IN SCIENCE

NUMBER 126 MAY 31, 1967

# A NEW SPECIES OF LATE OLIGOCENE DOG, *BRACHYRHYNCHOCYON SESNONI,* FROM SOUTH DAKOTA

*By* J. R. MACDONALD

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DAVID K. CALDWELL
*Editor*

# A NEW SPECIES OF LATE OLIGOCENE DOG, *BRACHYRHYNCHOCYON SESNONI,* FROM SOUTH DAKOTA

*By* J. R. MACDONALD[1]

ABSTRACT: *Brachyrhynchocyon sesnoni* is described from the middle of the Poleslide member of the Brule formation in the White River Badlands of South Dakota. Although younger than the genotypic species, *B. intermedius* (Loomis) from the Orellan of Wyoming, it is not the latest record of the genus as an undescribed species has been found in the overlying Arkikareean Sharps formation.

Recent collecting in the White River Badlands along the wall of the badlands on the south side of the White River by Los Angeles County Museum of Natural History field parties has been directed at finding ancestral forms of the mammalian species in the overlying Arikareean Sharps formation. A by-product of this effort was the expansion of the Museum's reference collection of Whitneyan forms and the discovery of several undescribed mammals. The specimen described below was found by Harley Garbani in 1964, while a Museum field party was working this area under the auspices of National Science Foundation Grant GB-3.

## **Brachyrhynchocyon sesnoni,** new species

Figures 1 and 2

*Type:* LACM 17039, partial skull with $I^3$ - $M^2$, canine - $M_3$, and miscellaneous skeletal fragments.

*Locality and Horizon:* LACM loc. no. 2002, Wolff Ranch Badlands, Shannon County, South Dakota. Poleslide member of Brule formation in ten foot red layer lying 110 to 120 feet above base of Poleslide member and 130 to 140 feet below the base of the Sharps formation.

*Diagnosis:* Premolars laterally compressed, $P_{3-4}$ with anterior cingular cusps and posterior accessory cusps, tall principal cusps; $M_3$ with subequal protoconid and metaconid, basined talonid; $P^{1-3}$ not crowded; palate tapered, $P^4$ with deuterocone extending slightly anterad of parastyle.

*Description:* $I^{1-2}$ missing; $I^3$ large, laterally compressed; separated from canine by diastema. Canine large, broken. $P^1$ small, laterally compressed; single cusped; single rooted; separated from canine and $P^2$ by short diastema. $P^2$ laterally compressed; apex of principal cusp above center of tooth; small posterior accessory cusp and posterior cingular cusp; separated from $P^3$ by short diastema. $P^3$ with greatest transverse diameter at principal cusp; apex of

[1]Senior Curator of Vertebrate Paleontology, Los Angeles Museum of Natural History.

*Figure 1. Brachyrhynchocyon sesnoni*, new species, LACM 17039. Partial cranium with $I^3$-$M^2$; palatal and labial views. (To be viewed with a stereoscope. Ca. X1.)

*Figure 2. Brachyrhynchocyon sesnoni*, new species, LACM 17039. Jaws with canine-$M_3$; occlusal and labial views. (To be viewed with a stereoscope. Ca. X1.)

TABLE 1

Measurements in millimeters of types of
*Brachyrhynchocyon sesnoni* and *B. intermedius*

| Character | *B. sesnoni* | | *B. intermedius* (after Loomis, 1931) |
|---|---|---|---|
| | Right | Left | |
| $I^3$ a-p | 4.4 | | |
| tr. | 3.0 | | |
| $P^1$ a-p | | 3.3 | |
| tr. | | 2.8 | |
| $P^2$ a-p | 7.1 | | |
| tr. | 3.05 | 2.85 | |
| $P^3$ a-p | 9.6 | 7.1 | |
| tr. | 4.3 | | |
| $P^4$ a-p (to parastyle) | 13.8 | 13.9 | |
| tr. | 8.3 | | |
| $M^1$ a-p | ca. 10.00 | | |
| tr. | ca. 15.00 | | |
| $M^2$ a-p | 5.6 | ca. 5.9 | |
| tr. | ca. 9.4 | ca. 8.8 | |
| $P^1$-$M^2$ | | 50.65 | 45.0 |
| $P_2$ a-p | | ca. 7.5 | |
| tr. | | 2.45 | |
| $P_3$ a-p | 8.4 | 8.7 | |
| tr. | 3.8 | 3.45 | |
| $P_4$ a-p | 9.9 | 10.1 | |
| tr. | 4.8 | 4.35 | |
| $M_1$ a-p | 15.2 | 15.6 | |
| tr. | 6.8 | ca. 6.8 | |
| $M_3$ a-p | | 5.0 | |
| tr. | | 3.8 | |
| $P_1$-$M_3$ | | ca. 55.6 | 53.0 |

principal cusp above anterior end of posterior root; small well-defined posterior accessory cusp and posterior cingular cusp. $P^4$ with small well-developed deuterocone extending antero-lingually, projecting slightly anterad of parastyle; parastyle broadly rounded; protocone and metastyle worn, separated by open carnassial notch. $M^1$ heavily worn; antero-labial corner less rounded, more angular than indicated by Loomis (1931: fig. 2). $M^2$ worn; paracone ane metacone subequal. $I_{1-2}$ missing. $I_3$ root only; laterally compressed. Canine broken; large. $P_1$ root only; separated from canine and $P_2$ by diastema. $P_2$ laterally compressed; low silhouette; apex of principal cusp worn away; small anterior and posterior accessory cusps; small posterior cingular cusp. $P_3$ similar to $P_2$; more robust; greatest transverse diameter between posterior cusps. $P_4$ slightly larger than $P_3$; greatest transverse diameter between principal cusp and posterior accessory cusp. $M_1$ heavily worn; paraconid and protoconid widely separated; metaconid small, extending slightly posterad of protoconid; talonid heavily worn, showing presence of strong hypoconid and moderately developed entoconid. $M_2$ worn to essentially featureless plain. $M_3$ greatly reduced; paraconid, if present, broken away; protoconid and metaconid form transverse crest; talonid slightly basined, opening labially. Symphysis long; extending to posterior end of $P_2$. Large mental foramen below center of $P_2$, small one below anterior edge of posterior root of $P_3$.

*Discussion:* The lower $P_{2-4}$ of *B. sesnoni* have anterior cingular cusps which are not found in *B. intermedius* (Loomis, 1931) but are found in an undescribed Wounded Knee-Sharps species; there is more lateral compression of these teeth than in the older and younger species. The $M_3$ has not been found in recorded specimens of the Brule species and is not as reduced as in the Sharps species. The canines in *B. sesnoni* do not dominate the symphysial region as they do in the Sharps form. The palate tapers from $P^4$ to $P^1$ while Loomis indicates an abrupt narrowing in *B. intermedius* at the $P^4$ with the anterior premolars in parallel rows.

The distal end of the humerus is somewhat catlike in aspect. It is flattened and laterally expanded with a wide internal condyle and a small entepicondylar foramen.

This species is named for Mr. William T. Sesnon, Jr., Chairman of the Board of Governors, Los Angeles County Museum of Natural History, and patron of Vertebrate Paleontology.

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DAVID K. CALDWELL
*Editor*

# A NEW SPECIES OF LATE OLIGOCENE DOG, *SUNKAHETANKA SHEFFLERI*, FROM SOUTH DAKOTA

*By* J. R. MACDONALD[1]

ABSTRACT: *Sunkahetanka sheffleri* is described from the Poleslide member of the Brule formation in the White River Badlands of South Dakota. This species is older than the genotypic species which is found in the Gering formation (*sensu* C. B. Schultz, *et al.*) of Nebraska and in the Sharps formation of South Dakota. It is less specialized than the later forms but does not give any greater indication of the origin of the genus.

The Vertebrate Paleontology Section of the Los Angeles County Museum of Natural History spent part of the summer of 1966 continuing its prospecting in the late Whitneyan and early Arikareean on the south side of the White River in Shannon County, South Dakota. The purpose of this program was to expand the Museum's reference collection and to look for ancestors of the forms which the writer has been collecting from the Arikareean Sharps formation. The specimen described below was found by Mr. Douglas J. Macdonald. The 1966 field season was supported by Mrs. E. Hadley Stuart, member of the Museum Board of Governors.

## **Sunkahetanka sheffleri,** new species

*Type:* LACM 17076, a partial skull with canine-$M^2$ and $P_1$ - $M_2$.

*Paratype:* LACM no. 17476, a cranium with $P^2$ - $M^2$.

*Locality and Horizon:* LACM no. 2006, Medicine Root Creek, Shannon County, South Dakota. Poleslide member of Brule formation, from twenty five feet of gray clays whose top is fifty nine feet below the base of the Sharps formation. These clays are overlain by *Protoceras* channels and underlain by a red clay. Late Whitneyan.

*Diagnosis:* Small, and teeth less massive than the genotypic species, *Sunkahetanka geringensis* (Barbour and Schultz); $M^{1-2}$ unreduced; $P_{2-3}$ with strong anterior cingular cusps.

*Description:* Canine broken. $P^1$ broken; small; single rooted; crowded between canine and $P^2$. $P^2$ set diagonally in tooth row; overlapping $P^1$ and $P^3$; no anterior cingular cusp; no posterior accessory cusp; posterior cingulum without cusp. $P^3$ set diagonally in tooth row; no anterior cingular cusp; principal cusp worn; small posterior accessory cusp. $P^4$ with broadly rounded parastyle; deuterocone prominent, lingual, but projecting slightly anterad of parastyle; protocone larger than metastyle; protocone-metastyle crest worn; closed carnassial notch below wear level. $M^1$ large; elongated transversely; paracone and metacone subequal; protoconule and metaconule worn; proto-

[1]Senior Curator of Vertebrate Paleontology, Los Angeles County Museum of Natural History.

*Figure 1. Sunkahetanka sheffleri,* new species, type, LACM 17076. Cranium with canine-$M^2$; lateral and palatal views. (To be viewed with a stereoscope. Ca. X-½.)

cone large, worn; hypocone large, worn. $M^2$ unreduced; paracone much larger than metacone, worn. Rostrum short; anterior edge of orbit above $P^4$ metastyle; sagittal crest not as strongly developed as in *S. geringensis*. $P_1$ small; single cusp; single root. $P_2$ with tall principal cusp; large anterior cingular cusp; posterior cingulum. $P_3$ similar to $P_2$; with posterior accessory cusp. $P_4$ similar to $P_3$. $M_1$ with short worn paraconid; closed carnassial notch; tall worn protoconid; small metaconid, projecting slightly posterad of protoconid; large hypoconids, worn virtually flat; small entoconid; thin enamel rim closes talinid basin on lingual side. $M_2$ broken; paraconid, if present, broken away; protoconid and metaconid worn flat, appear similar to $M_1$. $M_3$ missing. All teeth massive. The back of the paratype cranium is well preserved. The bullae are large, proportionally comparable to those of *S. geringensis;* the sagittal and lambdoidal crests and the occiput are smaller and less massive than those of the younger species.

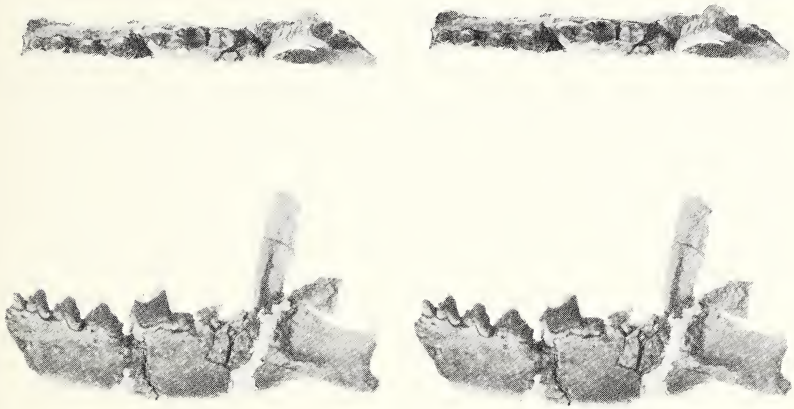

*Figure 2. Sunkahetanka sheffleri,* new species, type, LACM 17076. Left mandible with $P_1$-$M_2$; occlusal and labial views. (To be viewed with a stereoscope. Ca. X-½.)

*Discussion: Sunkahetanka geringensis* (Barbour and Schultz) (1935) is based on a skeleton collected from "fifteen feet above the Brule, 400 feet west of the road in Redington Gap, . . . west of Bridgeport, Morrill County, Nebraska." The beds are referred to the Gering formation by Barbour and Schultz although they are below the Gering formation as defined by Darton. Since 1953, eleven specimens (skulls, cranii, and mandibles) referable to this species have been found in the Sharps formation in the Wounded Knee area of Shannon County, South Dakota (Macdonald, 1963).

The Whitneyan specimens were found 310 feet stratigraphically below and 14 miles geographically from the nearest record of *S. geringensis*. This occurrence is a unique example of a species to species evolution in a restricted

TABLE 1

Measurements in millimeters of types of *Sunkahetanka*.

| Character | *Sunkahetanka sheffleri* | | | | *Sunkahetanka geringensis* | | | |
|---|---|---|---|---|---|---|---|---|
| | LACM 17076 Type | | LACM 17476 Paratype | | NSM* 4-28-8-31 | LACM 15910 | | SDSM** 5667 |
| | Right | Left | Right | Left | Type* | Right | Left | |
| $p^2$ a-p | | 7.95 | | 7.5 | 10.0 | 9.1 | 9.0 | |
| tr. | | 4.5 | | 3.4 | 5.2 | 5.0 | 5.1 | |
| $p^3$ a-p | | 9.7 | 8.4 | | 10.5 | 10.8 | 11.1 | |
| tr. | | 5.5 | 5.0 | | 6.2 | 6.0 | 6.0 | |
| $P^4$ a-p (to parastyle) | | 15.1 | 13.1 | | 16.0 | 17.2 | 17.0 | |
| tr. | 10.0 | | 8.8 | | 10.0 | 11.5 | 11.6 | |
| $M^1$ a-p | 11.4 | 11.5 | | | 11.5 | 9.9 | 11.1 | |
| tr. | | ca. 18.3 | | | 17.0 | 15.5 | 16.7 | |
| $M^2$ a-p | 6.2 | | | | 5.3 | 4.2 | 4.1 | |
| tr. | 11.0 | | | | 8.5 | 6.7 | 6.5 | |
| $P^1$-$M^2$ | | 52.8 | | | | 53.8 | 52.8 | |
| $P^{1-4}$ | | 38.8 | | | 40.0 | 42.5 | 40.9 | |
| $M^{1-2}$ (parastyle-metastyle) | | 18.2 | | | 17.0 | | 16.1 | |
| $P_1$ a-p | | 3.0 | | | 4.1 | | | |
| tr. | | 3.2 | | | 3.5 | | | |
| $P_2$ a-p | 7.2 | 6.5 | | | 8.0 | | | |
| tr. | 4.2 | 4.35 | | | 4.7 | | | |
| $P_3$ a-p | 8.55 | 8.8 | | | 9.0 | | | 8.0 |
| tr. | 5.0 | 5.05 | | | 5.5 | | | 4.8 |
| $P_4$ a-p | 10.5 | 10.2 | | | 11.3 | | | 10.1 |
| tr. | 58.85 | 6.5 | | | 6.5 | | | 6.5 |
| $M_1$ a-p | | 17.1 | | | 18.0 | | | 17.6 |
| tr. | | 7.8 | | | 8.2 | | | 7.6 |

*After Barbour & Schultze (1935:412) Nebraska State Museum.
**South Dakota School of Mines Museum of Geology.

area, the younger species replacing the older one in place during a relatively short span of geologic time, perhaps on the order of 2 to 3,000,000 years.

*S. geringensis* is slightly larger; the teeth are more massive; the $M^1$ has become moderately reduced; the $M^2$ greatly reduced; the jaw has become more massive and the sagittal crest, occiput, and lambdoidal crest much larger. These changes suggest a strengthening of the muscles for biting, chewing and manipulating the head. The general trend seems to be paralleling that seen in the *Tomarctus* - *Osteoborus* - *Borophagus* lineage of the Barstovian - Clarendonian - Hemphillian.

This species is named for Mr. William J. Sheffler, a member of the Board of Governors, Los Angeles County Museum of Natural History, and patron of Vertebrate Paleontology.

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# THE MARINE FISH FAUNA, BASED PRIMARILY ON OTOLITHS, OF A LOWER PLEISTOCENE DEPOSIT AT SAN PEDRO, CALIFORNIA (LACMIP 332, SAN PEDRO SAND)

*By* JOHN E. FITCH

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David K. Caldwell
*Editor*

# THE MARINE FISH FAUNA, BASED PRIMARILY ON OTOLITHS, OF A LOWER PLEISTOCENE DEPOSIT AT SAN PEDRO, CALIFORNIA (LACMIP 332, SAN PEDRO SAND)

*By* John E. Fitch[1]

Abstract: Several hundred pounds of fossiliferous "dirt," from a San Pedro sand deposit, yielded 2,746 otoliths, 584 vertebrae, 324 teeth, and 105 miscellaneous other fish remains representing at least 10 species of elasmobranchs and 30 kinds of teleosts. Since many of these fishes typically inhabit waters to the north of San Pedro, the deposit is believed to have been laid down during a period when ocean temperatures were colder than they are today at the same latitude. This deposit, one of the few remaining surface outcrops of San Pedro sand, will be destroyed by freeway construction prior to 1970.

The Miraflores Street deposit at San Pedro, California (LACMIP 332), was first brought to the attention of the Los Angeles County Museum of Natural History in 1963 by Roger D. Reimer, a student of paleontology with an especially keen interest in the Pliocene and Pleistocene of southern California. Museum personnel, under the supervision of George P. Kanakoff, then Curator of Invertebrate Paleontology, sampled the site extensively during ensuing months, but it was Reimer who found the first otoliths and called them to my attention.

Permission to sample the site was graciously granted by Jack Bell, owner of the property, and approximately 300 pounds of fossiliferous dirt were removed during two visits. This deposit is exposed at the base of a north-facing cliff, possibly 8 to 10 feet above present-day sea level, in the 600 block, Miraflores Street, San Pedro, California. The layer I sampled is composed primarily of friable molluscan remains in a fine, clean sandy matrix; it measures approximately 50 feet in a horizontal (east-west) direction by 18 to 24 inches vertically. Unfortunately, the Miraflores Street deposit is doomed by the impending southerly extension of the Harbor Freeway which is scheduled for completion prior to 1970. Until this occurs, it affords one of the last opportunities for the paleontologist to sample the San Pedro sand, and to learn of the various faunas represented by the contained assemblages.

When I processed my 300-pound field sample, as explained in a previous publication (Fitch, 1966b), I found the identifiable remains of 10 species of elasmobranchs and 30 teleosts. In addition to 2,746 otoliths, there were 584 vertebrae (9 from elasmobranchs), 324 teeth (99 from elasmobranchs), and 105 miscellaneous items: bone fragments, fin spines, dermal denticles, etc. (Table 1).

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TABLE 1. Fish Remains Found in a San Pedro Pleistocene Deposit (Miraflores Street)

| Scientific name | Common name | Type and number of remains | | | |
|---|---|---|---|---|---|
| | | otoliths | teeth | vertebrae | other |
| | ELASMOBRANCHS | | | | |
| *Carcharhinus* sp. | requiem shark | | 1 | | |
| *Galeorhinus zyopterus* | soupfin shark | | 9 | | |
| *Isurus oxyrinchus* | mako | | 1 | | |
| *Myliobatis californicus* | bat stingray | | 32 | | |
| *Notorynchus maculatus* | sevengill shark | | 6 | | |
| *Prionace glauca* | blue shark | | 3 | | |
| *Raja* spp. | skates | | 12 | | 6* |
| *Squalus acanthias* | spiny dogfish | | 19 | | |
| *Squatina californica* | Pacific angel shark | | 10 | | 8** |
| *Triakis semifasciata* | leopard shark | | 6 | | |
| | unidentified elasmobranchs | | | 9 | |
| | TELEOSTS | | | | |
| *Atherinops affinis* | topsmelt | 6 | | | |
| *Brosmophycis marginata* | red brotula | 1 | | | |
| *Chitonotus pugetensis* | roughback sculpin | 1 | | | |
| *Citharichthys sordidus* | Pacific sanddab | 22 | | | |
| *Citharichthys stigmaeus* | speckled sanddab | 191 | | | |
| *Citharichthys* spp. | sanddabs | 795 | | | |
| *Clupea pallasi* | Pacific herring | 29 | | | |
| *Coryphopterus nicholsi* | bluespot goby | 20 | | | |
| cottids | sculpins | 25 | | | |
| *Cymatogaster aggregata* | shiner perch | 1,129 | | | |
| *Engraulis mordax* | northern anchovy | 80 | | | |
| *Enophrys taurina* | bull sculpin | 1 | | | |
| *Eopsetta jordani* | petrale sole | 20 | | | |
| *Genyonemus lineatus* | white croaker | 2 | | | |
| *Glyptocephalus zachirus* | rex sole | 17 | | | |
| *Icelinus tenuis* | spotfin sculpin | 2 | | | |
| *Icichthys lockingtoni* | medusafish | 1 | | | |
| *Leptocottus armatus* | staghorn sculpin | 9 | | | |
| *Lycodopsis pacifica* | blackbelly eelpout | 12 | | | |
| *Lyopsetta exilis* | slender sole | 5 | | | |
| *Microgadus proximus* | Pacific tomcod | 1 | | | |
| *Oxyjulis californica* | señorita | 2 | | | |
| *Porichthys notatus* | plainfin midshipman | 148 | | | |
| *Radulinus asprellus* | slim sculpin | 3 | | | |
| *Rhacochilus vacca* | pile perch | 7 | | | |
| *Scorpaenichthys marmoratus* | cabezon | 1 | | | |
| *Sebastodes carnatus* | gopher rockfish | 1 | | | |
| *Sebastodes goodei* | chilipepper | 30 | | | |
| *Sebastodes* spp. | rockfish | 145 | | | |
| *Seriphus politus* | queenfish | 15 | | | |
| *Spirinchus starksi* | night smelt | 18 | | | |
| *Stenobrachius leucopsarus* | northern lampfish | 1 | | | |
| *Trachurus symmetricus* | jack mackerel | 3 | | | |
| | unidentified teleosts | 3 | 225 | 575 | 91† |

*"wing" spines
**dermal denticles
†pharyngeals, fin spines, opercula, etc.

Woodring, Bramlette and Kew (1946), using molluscan data, postulated that the San Pedro sand represented a shallow-water habitat in some localities, but other deposits contained moderate-depth mollusks not found elsewhere. These localities were inferred to represent depths of 25 to 50 fathoms.

Among the mollusks they identified from the San Pedro sand were six locally extinct northern species, but there were no locally extinct southern species. In addition, these deposits contain both northern and southern species that are now at or close to the limits of their range at the latitude of San Pedro. Based upon these and similar data, most geologists and paleontologists are prone to interpret the San Pedro sand as representing a portion of the Lower Pleistocene when local ocean temperatures were considerably colder than they are today.

Deposits of the San Pedro sand generally lie unconformably below the Palos Verdes sand, and in terms of events that took place during the time interval represented by the unconformity, there was "deformation; almost complete submergence or probably complete submergence of the area now constituting the Palos Verdes Hills; and intermittent emergence during which the series of marine terraces were formed and the marine deposits now found on most of them were laid down, the Palos Verdes sand constituting the marine deposits on the lowest and most extensive terrace on the landward side of the hills." (Woodring, Bramlette, and Kew, 1946).

## SYSTEMATIC ACCOUNT

### Hexanchidae—cow sharks

*Notorynchus maculatus* Ayres—sevengill shark

Although sevengill sharks range from northern British Columbia to San Carlos Point, Baja California, they seldom are seen or captured south of Point Conception. They reportedly attain lengths of 15 feet, but 7- to 9-foot specimens are quite large for California. A 5-foot 7-inch male caught at Santa Rosa Island in 1961 weighed 41 pounds. In southern California waters, individuals that size and smaller usually are caught at or near the bottom in depths exceeding 400 feet. Teeth of this species have been found in several Pliocene and Pleistocene deposits in southern California and in an Indian midden at Ventura, California (Fitch, 1964, In press, and unpublished data; Kanakoff, 1956).

*Material*: 6 teeth.

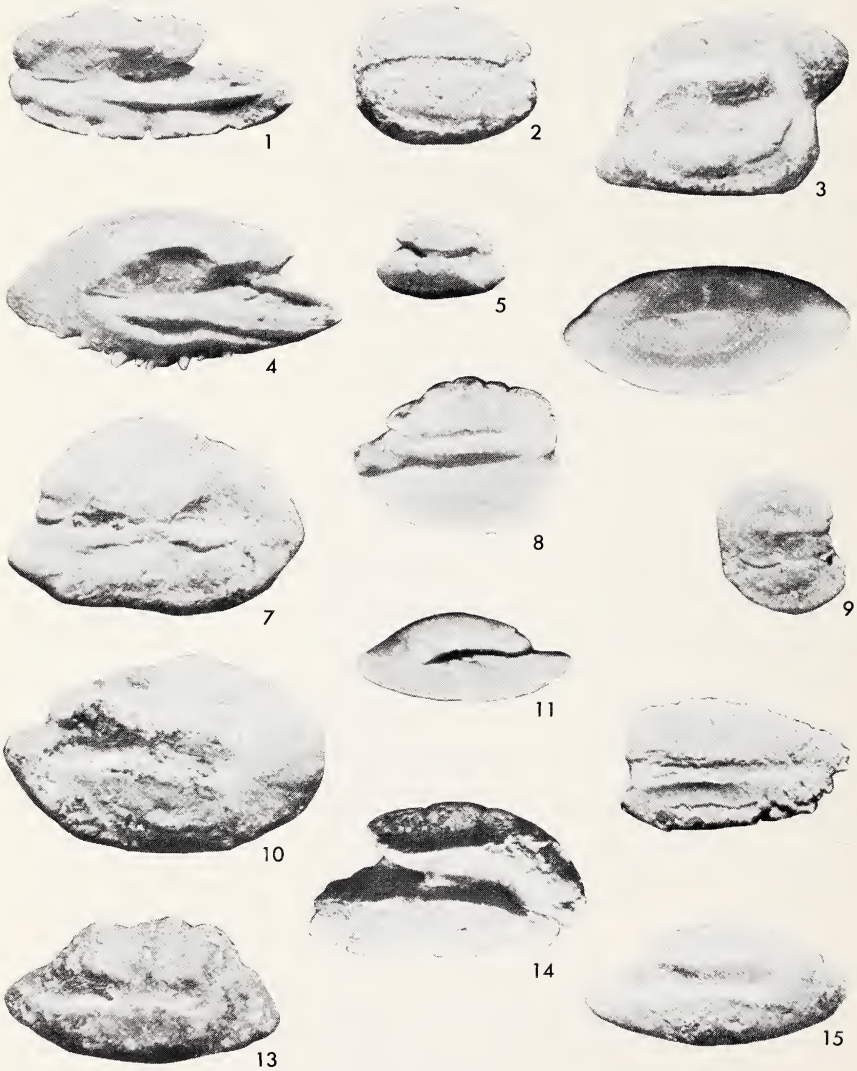
### Isuridae—mako sharks

*Isurus oxyrinchus* Rafinesque—mako

This world-ranging species is fairly common in our coastal waters between about San Francisco and Magdalena Bay, Baja California. Applegate (1966) reported an 11-footer from California that apparently represented a record

size for the species, but the usual mako in our waters is shorter than 8 feet. Mako remains, primarily teeth, have been found in numerous Pliocene and Pleistocene deposits in southern California (Fitch, 1964; and Kanakoff, 1956, as *I. glaucus;* Fitch, unpublished data) and in several coastal Indian middens (Fitch, In press; Follett, 1932, 1963a, 1963b).

*Material*: 1 tooth.



Carcharhinidae—requiem sharks

*Carcharhinus* sp.—requiem shark, species undetermined

At least four species of sharks belonging to the genus *Carcharhinus* have been captured off southern California at one time or another during the past four or five decades, but none of these tropical sharks occurs in any abundance north of about Magdalena Bay, Baja California. Although these sharks are rare visitors to our waters, all are common residents in tropical regions, especially around islands and offshore banks. A few members of this genus are pelagic forms, and some of these have worldwide distributions. Some species of requiem sharks may attain lengths of 15 feet, but others apparently never exceed 5. Because of confusion among taxonomists regarding speciation, it is difficult if not impossible to identify teeth beyond the generic level. *Carcharhinus* remains, mostly teeth, have been found in several Pliocene and Pleistocene deposits in southern California (Fitch, 1964, 1966b, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956).

*Material*: 1 tooth.

*Galeorhinus zyopterus* Jordan and Gilbert—soupfin shark

The soupfin shark ranges from northern British Columbia to about Magdalena Bay, but is not abundant at the more southerly latitudes. Females occur principally south of Point Conception, where they often are caught in depths as shallow as 100 feet. A 6½-foot female may weigh as much as 100 pounds, but 50- to 70-pounders are the usual sizes caught. Soupfin shark remains, mostly teeth, have been found in a number of Pliocene and Pleistocene deposits in southern California (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956, as *Triakis semifasciata*) and in several coastal Indian middens (Fitch, In press; Follett, 1963b).

*Material*: 9 teeth.

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*Figure 1*. Inner face, left sagitta of *Clupea pallasi* 3.7 mm long.
*Figure 2*. Inner face, left sagitta of *Atherinops affinis* 2.5 mm long.
*Figure 3*. Inner face, left sagitta of *Coryphopterus nicholsi* 3.8 mm long.
*Figure 4*. Inner face, left sagitta of *Engraulis mordax* 4.4 mm long.
*Figure 5*. Inner face, right sagitta of *Oxyjulis californicus* 1.7 mm long.
*Figure 6*. Inner face, right sagitta of *Brosmophycis marginata* 3.7 mm long.
*Figure 7*. Inner face, right sagitta of *Lycodopsis pacifica* 3.9 mm long.
*Figure 8*. Inner face, right sagitta of *Spirinchus starksi* 2.7 mm long.
*Figure 9*. Inner face, left sagitta of *Stenobrachius leucopsarus* 1.7 mm long.
*Figure 10*. Inner face, right sagitta of *Enophrys taurina* 4.3 mm long.
*Figure 11*. Inner face, left sagitta of *Chitonotus pugetensis* 2.8 mm long.
*Figure 12*. Inner face, right sagitta (badly worn, rostrum missing) of *Icichthys lockingtoni* 3.0 mm long.
*Figure 13*. Inner face, right sagitta of *Radulinus asprellus* 3.6 mm long.
*Figure 14*. Inner face, right sagitta (rostrum broken) of *Scorpaenichthys marmoratus* 3.7 mm long.
*Figure 15*. Inner face, right sagitta of *Icelinus tenuis* 3.5 mm long.

*Photographs by Jack W. Schott.*

*Prionace glauca* (Linnaeus)—blue shark

The blue shark is a pelagic species occurring in tropical, subtropical, and warm temperate areas of all world seas. On our coast, individuals sometimes stray into shallow water just outside the surf zone, but most are seen swimming slowly at the surface considerable distances offshore. Small blue sharks are extremely abundant off the California coast during summer months, and almost invariably these small sharks are males, indicating a geographical

distribution by sex. Although blue sharks are reported to reach lengths of 20 feet, the largest verified record was 12 feet 7 inches (Bigelow and Schroeder, 1948). Twelve-footers have been caught off our coast, but the usual blue shark in our waters is shorter than 6 feet and weighs less than 50 pounds. Blue shark remains are not abundant in fossil deposits, being known from only one other southern California locality (Lomita Marl Pliocene; Fitch, unpublished data). Follett (1963b) reported blue shark remains from a coastal Indian midden in Los Angeles County.

*Material*: 3 teeth.

Triakidae—smoothhounds

*Triakis semifasciata* Girard—leopard shark

The leopard shark has been caught between Oregon and Mazatlan, Mexico. It usually frequents shallow areas where the bottom is sandy, but also abounds in shallow rocky areas around southern California's offshore islands. The females grow larger than males and may reach lengths of 7 feet, but a 5-footer can be considered large. Leopard shark remains have been found in several Pliocene and Pleistocene deposits (Fitch, unpublished data; Fitch and Reimer, 1967) and in a few coastal Indian middens (Fitch, In press; Follett, 1963a, 1963b, 1964).

*Material*: 6 teeth.

Squalidae—dogfish sharks

*Squalus acanthias* Linnaeus—spiny dogfish

The spiny dogfish abounds in the north Pacific Ocean (eastern and western), ranging south on our coast to Sebastian Viscaino Bay, Baja California. Females attain larger sizes than males, and are reported to reach 5 feet, but a 4-footer can be considered large. Trawling off southern California yields best spiny dogfish catches in 100 to 250 feet of water, but they have been

*Figure 16*. Inner face, right sagitta of *Seriphus politus* 7.1 mm long.
*Figure 17*. Inner face, right sagitta of *Genyonemus lineatus* 3.8 mm long.
*Figure 18*. Inner face, left sagitta of *Citharichthys sordidus* 5.2 mm long.
*Figure 19*. Inner face, right sagitta of *Sebastodes carnatus* 11.6 mm long.
*Figure 20*. Inner face, right sagitta of *Rhacochilus vacca* 7.8 mm long.
*Figure 21*. Inner face, left sagitta of *Citharichthys stigmaeus* 3.2 mm long.
*Figure 22*. Inner face, right sagitta of *Sebastodes goodei* 12.1 mm long.
*Figure 23*. Inner face, right sagitta of *Cymatogaster aggregata* 4.7 mm long.
*Figure 24*. Inner face, right sagitta of *Glyptocephalus zachirus* 4.7 mm long.
*Figure 25*. Inner face, right sagitta of *Leptocottus armatus* 6.6 mm long.
*Figure 26*. Inner face, right sagitta of *Porichthys notatus* 5.4 mm long.
*Figure 27*. Inner face, left sagitta of *Eopsetta jordani* 4.7 mm long.
*Figure 28*. Inner face, left sagitta (rostrum missing) of *Trachurus symmetricus* 6.8 mm long.
*Figure 29*. Inner face, left sagitta of *Microgadus proximus* 6.8 mm long.
*Figure 30*. Inner face, left sagitta of *Lyopsetta exilis* 3.2 mm long.
*Photographs by Jack W. Schott.*

caught both shallower and deeper. Remains of *Squalus acanthias* have been found in numerous Pliocene and Pleistocene deposits in southern California (Fitch, unpublished data; Fitch and Reimer, 1967) and in an Indian midden at Ventura, California (Fitch, In press).

*Material*: 19 teeth.

Squatinidae—angel sharks

*Squatina californica* Ayres—Pacific angel shark

Although the Pacific angel shark ranges from southern Alaska into the Gulf of California, it apparently is not abundant north of Point Conception nor south of Magdalena Bay. Skin divers often observe them buried in sand or mud at depths of 8 to 150 feet or more, but greatest concentrations are noted in 50 to 70 feet. They are reported to attain lengths of about 5 feet, but the largest I have examined, a 44-inch female, weighed 31 pounds. Pacific angel shark remains have been found in numerous Pliocene and Pleistocene deposits in southern California (Fitch, 1964, and unpublished data) and in several coastal Indian middens (Fitch, In press; Follett, 1932, 1963a, 1963b).

*Material*: 10 teeth and 8 dermal denticles.

Rajidae—skates

*Raja* spp.—skates, species undetermined

Although six species of skates (at least) occur off California, I was unable to find foolproof characters for distinguishing the teeth of any one of these from those of the other five. By size alone, teeth of large *R. binoculata* can be distinguished if they are present, but no really large skate teeth were found in the Miraflores Street deposit. At various times, skates can be captured at all depths from the shallow subtidal to those exceeding several thousand feet. Skate remains have been found in numerous Pliocene and Pleistocene deposits in southern California (Fitch, 1964, and unpublished data) and in an Indian midden at Ventura, California (Fitch, In press).

*Material*: 12 teeth and 6 "wing spines."

Myliobatidae—eagle rays

*Myliobatis californicus* Gill—bat stingray

Bat stingrays range from Oregon to Magdalena Bay, occurring in shallow bays, along the mainland coast, and around offshore islands. A record specimen weighed 209 pounds, but individuals exceeding 50 pounds are rare. Remains of *M. californicus*, primarily teeth, have been found in many Pliocene and Pleistocene deposits in southern California (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956), and in several coastal Indian middens (Fitch, In press; Follett, 1963b; Harrington, 1928).

*Material*: 32 teeth.

### Unidentified elasmobranchs

No effort was made to assign family or generic names to the nine small elasmobranch vertebrae recovered from this deposit. It is presumed that they came from some of the same species as the teeth that were found.

### Clupeidae—herrings

*Clupea pallasi* Valenciennes—Pacific herring

The Pacific herring ranges throughout the north Pacific Ocean (western and eastern), but because of pollution and bay development, is no longer important on our coast south of Point Conception, although it may still occur in small numbers as far south as Ensenada, Baja California. They are said to attain lengths of 18 inches, but a 12- to 14-inch individual can be considered large; a fish of this size will weigh about a pound. Pacific herring otoliths have been found in several Pliocene and Pleistocene deposits in southern California (Fitch, unpublished data). The sagittae of a large, adult Pacific herring will exceed 5.0 mm in length.

*Material*: 29 otoliths 2.1 to 4.8 mm long (Fig. 1).

### Engraulidae—anchovies

*Engraulis mordax* Girard—northern anchovy

The northern anchovy is a schooling fish that ranges from British Columbia to Magdalena Bay and offshore for more than 100 miles. They are reported to attain lengths of 9 inches, but a 7-inch individual can be considered unusually large. Otoliths of *E. mordax* have been found in many Pliocene and Pleistocene deposits in southern California (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967), and in Indian middens at Ventura and Corona del Mar (Fitch, In press). The sagittae of a large, adult northern anchovy will exceed 4.5 mm in length.

*Material*: 80 otoliths 1.9 to 4.7 mm long (Fig. 4).

### Osmeridae—smelts

*Spirinchus starksi* (Fisk)—night smelt

The night smelt ranges from Shelikof Bay, southeastern Alaska to Point Arguello, California. It is reported to attain a length of 9 inches, but individuals exceeding 7 inches are rarely encountered. McAllister (1963) in revising the smelt family (Osmeridae) mentions that only one genus (*Mallotus*) has a fossil record. I have found *S. starksi* remains only at one other site, a marine Pliocene deposit at Santa Barbara, California, but osmerid otoliths (apparently *Spirinchus* sp.) are abundant in a freshwater Pliocene deposit (Tulare formation) in Kettleman Hills, California (Fitch, unpublished data). The sagittae of a large, adult night smelt will exceed 4.5 mm in length.

*Material*: 18 otoliths 2.1 to 3.3 mm long (Fig. 8).

Myctophidae—lanternfishes

*Stenobrachius leucopsarus* (Eigenmann and Eigenmann)—northern lampfish

*S. leucopsarus* is one of the most abundant bathypelagic fishes in the eastern north Pacific, where it ranges from the Bering Sea to about Cedros Island, Baja California. A large individual might be 5 inches long and weigh about one-half ounce. Otoliths of this species have been found in many Pliocene and Pleistocene deposits in southern California, more than 1,000 having been recovered from a San Pedro, California, (Lomita Marl) deposit (Fitch, 1966b, and unpublished data). The sagittae of a large, adult northern lampfish will exceed 1.8 mm in length.

*Material*: 1 otolith 1.7 mm long (Fig. 9).

Gadidae—cods

*Microgadus proximus* (Girard)—Pacific tomcod

The Pacific tomcod ranges from Alaska to about Morro Bay, California, usually at depths of 200 feet or more, but sometimes in shallow water just outside the surf zone. They are reported to reach lengths of 12 inches, but no weights are available for such a fish; a 10¼-inch female weighed just under 6 ounces. *M. proximus* otoliths are rare in southern California Pliocene and Pleistocene deposits, but are abundant in the Pleistocene of Oregon (Fitch, unpublished data). The sagittae of a large, adult Pacific tomcod will exceed 14.0 mm in length.

*Material*: 1 otolith 6.8 mm long (Fig. 29).

Bothidae—lefteyed flounders

*Citharichthys sordidus* (Girard)—Pacific sanddab

Pacific sanddabs are reported to range from southern Alaska to about Magdalena Bay, but the occurrence of the species in central and southern Baja California needs to be verified. The maximum length and weight attributed to *C. sordidus* (16 inches and 2 pounds) also are questionable. A 12-inch female, the largest of several thousand Pacific sanddabs recently examined, weighed less than 10 ounces. *Citharichthys* otoliths are abundant in southern California Pliocene and Pleistocene deposits, and many of these are from *C. sordidus* (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967). The sagittae of a large, adult Pacific sanddab will exceed 8.0 mm in length.

*Material*: 22 otoliths 2.5 to 5.9 mm long (Fig. 18).

*Citharichthys stigmaeus* Jordan and Gilbert–speckled sanddab

Speckled sanddabs range along the coast from southeastern Alaska to Sebastian Viscaino Bay, Baja California, usually in depths shallower than 200 feet, and often just outside the surf zone. A large individual, about 5 inches long, would weigh less than an ounce. *C. stigmaeus* otoliths have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964,

and unpublished data; Fitch and Reimer, 1967), and in an Indian midden at Ventura (Fitch, in press). The sagittae of a large, adult speckled sanddab will exceed 3.5 mm in length.

*Material*: 191 otoliths 1.5 to 3.4 mm long (Fig. 21).

*Citharichthys* spp.—sanddabs, species undetermined

The otoliths of all three species of *Citharichthys* known to California are easily distinguished if they are in good condition, but most fossil sanddab otoliths are either worn, fragmented, or partially digested, making specific identification impossible. Some of the unidentified sanddab otoliths in this deposit could have been from *C. xanthostigma* (the third California species), but most of them probably were from Pacific and speckled sanddabs.

*Material*: 795 otoliths identifiable to genus only.

Pleuronectidae—righteyed flounders

*Glyptocephalus zachirus* Lockington—rex sole

The rex sole ranges from the Bering Sea to Ensenada, Baja California (at least) in depths from shallow water to 2,100 feet. They are reported to attain lengths of 22 inches, but no weights are available for fish that size; a 15-inch female weighed just under 1½ pounds. Rex sole otoliths are abundant in some southern California Pliocene and Pleistocene deposits, more than 700 having been recovered from the Lomita Marl (Pliocene) at San Pedro (Fitch, unpublished data). The sagittae of a large, adult rex sole will exceed 7.0 mm in length.

*Material*: 17 otoliths 1.5 to 4.7 mm long (Fig. 24).

*Lyopsetta exilis* (Jordan and Gilbert)—slender sole

The slender sole ranges from southeastern Alaska to Cedros Island, usually in depths of 400 to 800 feet, but sometimes as shallow as 120 feet or as deep as 1,700. A large individual might exceed 12 inches in length, but probably would not weigh more than ¼ pound. Otoliths of *L. exilis* have been found in numerous southern California Pliocene and Pleistocene deposits (Fitch, 1964; Fitch and Reimer, 1967), more than 2,000 having been recovered from the Lomita Marl at San Pedro (Fitch, unpublished data). The sagittae of a large, adult slender sole will exceed 5.5 mm in length.

*Material*: 5 otoliths 2.6 to 4.2 mm long (Fig. 30).

*Eopsetta jordani* (Lockington)—petrale sole

The petrale sole ranges from northwestern Alaska to south of Ensenada, at least, migrating annually between deep and shallow water. They are reported to attain a length of 25¼ inches and a weight of 8 pounds or more, but a 5-pounder is considered quite large by most commercial fishermen. The otoliths of *E. jordani* are difficult to distinguish from those of two other eastern Pacific flatfishes, *Parophrys vetulus* and *Lepidopsetta bilineata,* unless they

are in perfect or near perfect condition. Since several of the "*Eopsetta*" otoliths from this deposit were in relatively poor condition, a few may not be properly assigned. The sagittae of a large, adult petrale sole will exceed 10.0 mm in length.

*Material*: 20 otoliths 2.0 to 5.8 mm long (Fig. 27).

Atherinidae—silversides

*Atherinops affinis* (Ayres)—topsmelt

Topsmelt range from the Straits of Juan de Fuca to and into the Gulf of California. Various subspecies inhabit bays, kelp beds, and offshore island areas where they live at or near the surface. A 14½-inch female weighing slightly less than 12 ounces appears to be a record size. Topsmelt otoliths have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, and unpublished data), and in an Indian midden at Ventura (Fitch, In press). The sagittae of a large, adult topsmelt will exceed 5.0 mm in length.

*Material*: 6 otoliths 1.7 to 4.0 mm long (Fig. 2).

Carangidae—jacks

*Trachurus symmetricus* (Ayres)—Pacific jackmackerel

The Pacific jackmackerel, a schooling fish, is perhaps one of the three or four most abundant species off our coast, ranging from British Columbia to Cape San Lucas and offshore for several hundred miles. The commercial catch is comprised primarily of fish shorter than 15 inches, but jackmackerel are known to attain lengths of 30 inches and weights of 5 pounds or more. *T. symmetricus* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1966b, and unpublished data), and in an Indian midden at La Jolla (Fitch, unpublished data). The sagittae of a large, adult Pacific jackmackerel will exceed 10.0 mm in length.

*Material*: 3 otoliths longer than 6.0 mm (Fig. 28).

Centrolophidae—medusaefishes

*Icichthys lockingtoni* Jordan and Gilbert—medusafish

The medusafish ranges throughout the offshore area between British Columbia and central Baja California. Very young individuals (to perhaps 3 or 4 inches) usually accompany jellyfishes, apparently enjoying some type of commensal relationship. Large individuals (10 to 12 inches long) do not seem to associate with medusae, solitary specimens occasionally being captured in mid-water trawls and other nets. I have not encountered *I. lockingtoni* remains in any other fossil deposit. The sagittae of a large, adult medusafish will exceed 10.0 mm in length.

*Material*: 1 otolith (Fig. 12) in poor condition, longer than 3.0 mm.

Sciaenidae—croakers

*Genyonemus lineatus* (Ayres)—white croaker

The white croaker ranges from Vancouver Island to Magdalena Bay, abounding in almost every type of habitat between the intertidal and depths of 600 feet. A near-record 14½-inch fish weighed 1.4 pounds. White croaker sagittae frequently are the most abundant fish remains in southern California Pliocene and Pleistocene deposits, comprising 6,409 of the more than 11,000 otoliths recovered from a San Diego Pliocene locality (San Diego Formation, unpublished data). They are also a common constituent of many coastal Indian middens: Fitch (In press) reports 7,655 *G. lineatus* otoliths from an Indian midden at Ventura. In view of their abundance in other deposits, their scarcity in this deposit (Miraflores Street) is difficult to explain. The sagittae of a large, adult white croaker will exceed 12.5 mm in length.

*Material*: 2 otoliths (Fig. 17) in poor condition, longer than 3.8 mm.

*Seriphus politus* Ayres—queenfish

Queenfish range from Yaquina Bay, Oregon, to San Juanico Bay, Baja California, living in much the same habitat as the white croaker. A near-record 12-inch female weighed just over 10 ounces. Queenfish otoliths have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956), and in several coastal Indian middens (Fitch, In press). The sagittae of a large, adult queenfish will exceed 10.0 mm in length.

*Material*: 15 otoliths 2.7 to 7.1 mm long (Fig. 16).

Embiotocidae—surfperches

*Cymatogaster aggregata* Gibbons—shiner perch

The shiner perch ranges from Port Wrangel, Alaska, to Santo Tomas Point, Baja California, being restricted to the mainland coast, primarily in depths shallower than 50 feet, but occasionally trawled in 400 feet. A record-sized pregnant female 7 inches long, weighing just under 3 ounces, contained 16 young which were almost 2 inches long each. Although *C. aggregata* otoliths have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967), they usually comprise less than 10 percent of the total sagittae recovered. In this deposit, they made up almost 50 percent of the more than 2,700 otoliths found. The sagittae of a large, adult shiner perch will exceed 6.5 mm in length.

*Material*: 1,129 otoliths 2.0 to 6.4 mm long (Fig. 23).

*Rhacochilus vacca* (Girard)—pile perch

The pile perch ranges from Port Wrangel, Alaska, to San Martin Island, Baja California, primarily in shallow water around kelp beds, pier and dock pilings, breakwaters, and similar habitat. A near-record 17-inch female weighed just under 4 pounds. Pile perch remains, mostly otoliths and pharyn-

geal teeth, have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data), and in an Indian midden at Ventura (Fitch, In press). The sagittae of a large, adult pile perch will exceed 9.5 mm in length.

*Material*: 7 otoliths 6.6 to 9.9 mm long (Fig. 20).

Labridae—wrasses

*Oxyjulis californica* (Günther)—señorita

The señorita ranges from Natural Bridges State Park to Cedros Island, inhabiting shallow areas of rocky substrate and similar relief where kelp beds and other vegetation grows. A near-record 9-inch male speared at Dana Point in January 1965 weighed 4 ounces. Señorita otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult señorita will exceed 3.5 mm in length.

*Material*: 2 otoliths 1.7 to 2.2 mm long (Fig. 5).

Scorpaenidae—rockfishes

*Sebastodes carnatus* (Jordan and Gilbert)—gopher rockfish

The gopher rockfish ranges from Eureka, California, to San Roque, Baja California, living almost exclusively in areas of rocky substrate from the shallow subtidal to depths of 180 feet. The species is reported to attain a length of 15 inches, but the largest I have seen was a 12-incher that weighed an ounce over 1 pound. The otoliths of *S. carnatus* are not known from any other fossil deposit. The sagittae of a large, adult gopher rockfish will exceed 11.5 mm in length.

*Material*: 1 otolith 11.6 mm long (Fig. 19).

*Sebastodes goodei* Eigenmann and Eigenmann—chilipepper

The chilipepper ranges from Vancouver Island to Magdalena Bay, usually at depths greater than 600 feet. A 20½-inch female (1½ inches short of the reported maximum) caught at Cortez Bank in December 1964 weighed just under 4 pounds. *S. goodei* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult chilipepper will exceed 17.0 mm in length.

*Material*: 30 otoliths 6.0 to 12.1 mm long (Fig. 22).

*Sebastodes* spp.—rockfishes, species undetermined

The otoliths of most of the 52 members of the genus *Sebastodes* inhabiting the waters of California, can be distinguished one from the other if they are from adult fish, and if they are not worn or broken. Such characters as length and shape of rostrum, configuration of posterior end, presence or absence of marginal frills, angle of posterior taper, depth of sulcus, and number of growth zones (annuli) for otolith length are helpful for identify-

ing sagittae of the various species or species-complexes. Unfortunately, very few fossil otoliths are sufficiently well preserved to be identified to species.

*Material*: 145 otoliths, probably representing four or five species, at least.

Cottidae—sculpins

*Chitonotus pugetensis* (Steindachner)—roughback sculpin

The roughback sculpin ranges from northern British Columbia to Magdalena Bay, usually at depths of 100 to 350 feet, but sometimes shallower or deeper. A large individual might be 7 inches long and weigh about 2 ounces. *C. pugetensis* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1964, and unpublished data). The sagittae of a large, adult roughback sculpin will exceed 6.0 mm in length.

*Material*: 1 otolith 2.8 mm long (Fig. 11).

*Enophrys taurina* Gilbert—bull sculpin

The bull sculpin ranges from Monterey Bay to Anacapa Island, usually at depths of 100 to 250 feet, but sometimes as shallow as 30 feet or as deep as 800. A 6-inch specimen (perhaps near maximum size) will weigh about 2 ounces. *E. taurina* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of an adult bull sculpin will exceed 5.5 mm in length.

*Material*: 1 otolith 4.3 mm long (Fig. 10).

*Icelinus tenuis* Gilbert—spotfin sculpin

The spotfin sculpin ranges from Queen Charlotte to Guadalupe Island, Baja California, usually in depths of 100 to 400 feet, but some have been taken as shallow as 50 feet and as deep as 1,200. These small, slender fishes (4 inches might be about maximum length) probably never attain a weight of one ounce, even when full of eggs. Their otoliths are extremely difficult to distinguish from those of the yellowchin sculpin, *I. quadriseriatus,* but a critical comparison indicates *I. tenuis* sagittae are somewhat more pointed posteriorly, are more slender (height into length), and have a slightly less-pronounced rostrum. Since all of these characters are relative, it is necessary to compare each fossil otolith with an assortment of similar sized sagittae from living fishes before specific names can be assigned. Even with such critical evaluation, 100 percent accuracy is not assured. Otoliths of both these species of *Icelinus* are abundant in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult spotfin sculpin will exceed 4.5 mm in length.

*Material*: 2 otoliths 3.0 to 3.5 mm long (Fig. 15).

*Leptocottus armatus* Girard—Pacific staghorn sculpin

The Pacific staghorn sculpin ranges from northwestern Alaska to San Quintin Bay, Baja California, being particularly common in shallow outer

coast waters, and in bays and lagoons. It is reported to reach a length of 12 inches, but the largest I have seen was a 10-inch female netted in 1958 that weighed 8 ounces. *L. armatus* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data), and in an Indian midden at Ventura (Fitch, In press). The sagittae of a large, adult staghorn sculpin will exceed 9.0 mm in length.

*Material*: 9 otoliths 3.1 to 6.6 mm long (Fig. 25).

*Radulinus asprellus* Gilbert—slim sculpin

The slim sculpin ranges from Kodiak Island, Alaska, to about Ensenada, Baja California, usually at depths exceeding 150 feet. A 5½-inch fish (large for the species) will weigh about 1 ounce. Otoliths of *R. asprellus* have been found in a number of southern California Pliocene and Pleistocene deposits, over 1,300 having been recovered from a Pliocene site (Lomita Marl) at San Pedro (Fitch, unpublished data). The sagittae of a large, adult slim sculpin will exceed 4.0 mm in length.

*Material*: 3 otoliths 3.2 to 3.6 mm long (Fig. 13).

*Scorpaenichthys marmoratus* (Ayres)—cabezon

The cabezon ranges from northern British Columbia to Abreojos, Baja California, primarily in areas where the bottom is rocky, but often over sandy or sandy-mud substrate also. The cabezon is reported to reach a length of 39 inches (Miller, Gotshall, and Nitsos, 1965) and a weight of 20 to 25 pounds (Roedel, 1953), but individuals exceeding 25 inches and 10 pounds are rare. Cabezon otoliths have not been found in any other fossil deposit. The sagittae of a large, adult cabezon will exceed 6.5 mm in length.

*Material*: 1 otolith (Fig. 14), in poor condition, longer than 3.7 mm.

Unidentified sculpins

A number of otoliths and otolith fragments were identifiable as sculpins (family Cottidae), but were not in good enough condition to determine genus or species.

*Material*: 25 badly worn otoliths.

## Gobiidae—gobies

*Coryphopterus nicholsi* (Bean)—bluespot goby

The bluespot goby ranges from British Columbia to San Martin Island. Although the adults are bottom dwellers in the shallow subtidal and to depths of about 200 feet, larvae and juveniles sometimes are taken in plankton nets 100 miles or more offshore (Ebert and Turner, 1962). *C. nicholsi* seldom exceeds a length of 5 inches or a weight of 1 ounce. Their otoliths have been found in many southern California Pliocene and Pleistocene deposits, over 1,700 having been recovered from a Pliocene site (Lomita Marl) at San Pedro

(Fitch, unpublished data). The sagittae of a large, adult bluespot goby will exceed 3.0 mm in length.

*Material*: 20 otoliths 1.8 to 3.8 mm long (Fig. 3).

Batrachoididae—toadfishes

*Porichthys notatus* Girard—plainfin midshipman

The plainfin midshipman ranges from southeastern Alaska to Cedros Island, being one of the half-dozen most abundant species at depths of 300 to 750 feet. During spawning and "nesting" they often move into intertidal areas, but during other periods they may travel into depths of 1,200 feet or more. *P. notatus* is reported to attain a length of 15 inches, but the largest I have seen was a 13½-inch male weighing just over 14 ounces. Plainfin midshipman sagittae often are one of the most abundant otoliths in southern California Pliocene and Pleistocene deposits, nearly 700 having been recovered from a Pliocene site (Lomita Marl) at San Pedro (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967). The sagittae of a large, adult plainfin midshipman will exceed 10.0 mm in length.

*Material*: 148 otoliths 0.7 to 7.9 mm long (Fig. 26).

Zoarcidae—eelpouts

*Lycodopsis pacifica* (Collett)—blackbelly eelpout

The blackbelly eelpout ranges from the Gulf of Alaska to Ensenada (at least), being very abundant in trawl catches made in depths of 100 to 800 feet or more. It is reported to attain a length of 18 inches and a weight of about 1/3 pound. *L. pacifica* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult blackbelly eelpout will exceed 5.0 mm in length.

*Material*: 12 otoliths 2.2 to 5.1 mm long (Fig. 7).

Brotulidae—brotulas

*Brosmophycis marginata* (Ayres)—red brotula

The red brotula ranges from southeastern Alaska to Ensenada, at least, mostly in depths of 60 to 400 feet in areas where a rocky bottom offers an opportunity for concealment. Although some individuals may reach lengths of 18 inches, few specimens are seen that exceed 16 inches or about 12 ounces. *B. marginata* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult red brotula will exceed 14.0 mm in length.

*Material*: 1 otolith 3.7 mm long (Fig. 6).

Unidentified teleosts

Three badly deteriorated otoliths, 225 teeth, 575 vertebrae, and 91 assorted bone fragments recovered from this deposit could not be identified at

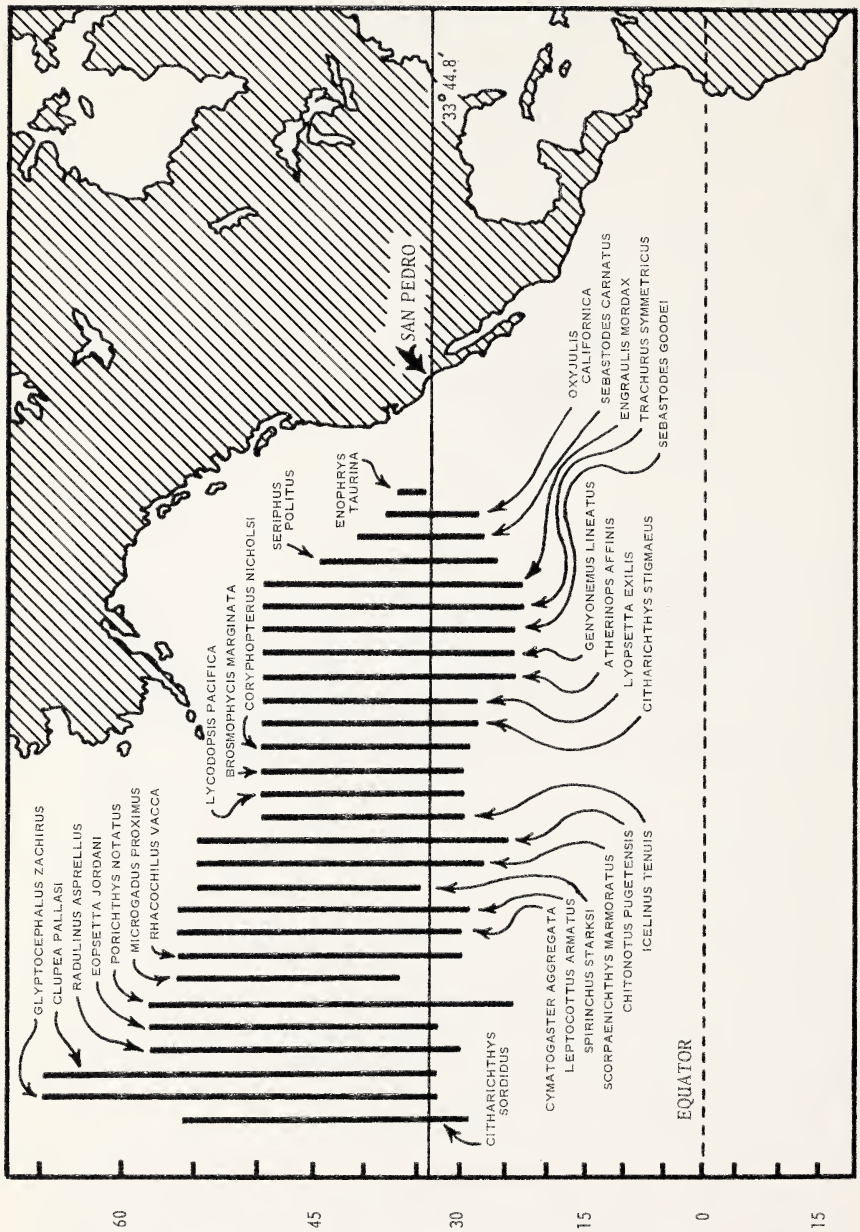


*Figure 31.* Present-day distributions of the 28 non-bathypelagic bony fishes identified from the Miraflores Street, San Pedro, California deposit (lat. 33° 44.8′ N.)

this time except as "teleosts." Most of these remains are presumed to have come from the same species that "left" their otoliths.

## DISCUSSION

Possibly 5 of the 40 fish species identified from the Miraflores Street deposit might be considered northern forms, 1 a "southerner," and 3, offshore or pelagic species. Two of the northern species, *Notorynchus maculatus* and *Clupea pallasi,* occasionally have been noted south as far as the latitude of this deposit during modern times, but the known ranges of *Spirinchus starksi, Microgadus proximus,* and *Enophrys taurina* all terminate to the north of San Pedro (Fig. 31).

Several species of *Carcharhinus* are abundant in waters off southern Baja California, but only during warm summer months or years when local water temperatures are higher than normal do a few individuals stray into the southern California area.

Two of the three offshore species, *Prionace glauca* and *Icichthys lockingtoni,* sometimes are captured in or near the surf zone, but these may be sick individuals, because such behavior is not believed normal for either. Typically they are found in clear, blue offshore waters, generally in the upper 50 meters of the water column. *Stenobrachius leucopsarus,* the third "offshore" species, seldom is captured in water shallower than 1,000 feet, yet its otoliths were found in five of eight marine Pliocene and Pleistocene deposits that I have sampled extensively. In three of these five deposits, only one *Stenobrachius* otolith was recovered, but in the other two, Timms Point silt and Lomita marl, they were more abundant.

In many respects, the Miraflores Street fish fauna is similar to what I found in both the Timms Point silt and the Lomita marl, yet in the proportion of surfperch otoliths (Embiotocidae) it is unique among all the deposits I have investigated. Three species, *Clupea pallasi, Radulinus asprellus,* and *Brosmophycis marginata,* were present only in these three coldwater deposits. Four other species, *Stenobrachius leucopsarus, Trachurus symmetricus, Coryphopterus nicholsi,* and *Lycodopsis pacifica,* were present only in these same three deposits plus one or at most two other deposits. (All but *Trachurus* were in the San Diego Pliocene, and *Stenobrachius* and *Trachurus* were both in the Playa del Rey Pleistocene.) A similarity also is seen in the insignificant role of *Genyonemus lineatus* and *Seriphus politus* otoliths in the Miraflores Street, Timms Point silt, and Lomita marl deposits. *Genyonemus* contributed 0, 8, and 2 otoliths respectively to the total otolith yield for these three "coldwater" deposits, while only 15, 8, and 3 *Seriphus* otoliths were recovered. In the five "non-coldwater" deposits that were sampled extensively (Table 2), *Genyonemus* otoliths were very important, comprising from 13 (Playa del Rey) to 55 (Signal Hill and San Diego Pliocene) percent of the total recovered. *Seriphus* otoliths were also very important in these same five deposits.

TABLE 2. Otolith Yield from Eight Heavily-Sampled, Southern California Pliocene and Pleistocene Deposits

| Deposit Locality | Designation | Age | Otoliths recovered |
|---|---|---|---|
| Signal Hill (LACMIP 423 | ? | Pliocene | 1,230* |
| San Diego (LACMIP 305) | San Diego fm. | Pliocene | 11,590* |
| Miraleste Canyon (LACMIP 435) | Lomita marl | Pliocene | 24,299† |
| Timms Point (LACMIP 130) | Timms Point silt | Lower Pleistocene | 2,370** |
| Miraflores Street (LACMIP 332) | San Pedro sand | Lower Pleistocene | 2,746† |
| Playa del Rey (LACMIP 59) | Palos Verdes sand | Upper Pleistocene | 2,591** |
| 500 block N. Pacific (LACMIP 131) | Palos Verdes sand | Upper Pleistocene | 662† |
| 700 block N. Pacific | Palos Verdes sand | Upper Pleistocene | 282† |

*recovered "by eye."

**about one-half recovered "by eye" and one-half with microscope.

†recovered with microscope.

In view of the similarities between otoliths from the Miraflores Street deposit and those recovered from the Timms Point silt and Lomita marl, I feel certain that additional sampling would yield many more species, particularly such northern forms as are unique to Timms Point and Lomita marl (*e.g., Atheresthes stomias, Malacocottus zonurus, Icelinus burchami, Lyconectes aleutensis, Ammodytes hexapterus,* etc.).

No explanation is readily available as to why *Cymatogaster aggregata* otoliths comprised 41 percent of the total otolith yield of the Miraflores Street deposit. In no other deposit I have examined did surfperch otoliths exceed 10 percent of the total; however, a high yield of *Cymatogaster* otoliths was obtained in a 4-quart sediment sample from Ship Rock, on the leeward side of Santa Catalina Island, California. Department of Fish and Game biologist-divers had scooped up this sample (representing a sheltered environment) in 125 feet of water during routine diving operations, and saved it for me to examine. Sediment samples from exposed coastal areas have never yielded a disproportionate number of embiotocid otoliths, so such a phenomenon may exemplify deposition in a sheltered environment at moderate depth.

Interestingly, otoliths of *Otophidium taylori* were entirely lacking in the Miraflores Street deposit, yet they were important or very important in every other Pliocene and Pleistocene deposit sampled, and a few were found in the sediment sample from Ship Rock. This is not a reflection of inadequate sampling or poor recovery techniques at Miraflores Street—*O. taylori* otoliths simply were not present! Since most fossil assemblages represent death associations, rather than life associations, the lack of *O. taylori* otoliths cannot be construed as positive proof the species was not an integral part of the fauna of the period, but it is a good indication that it was not.

I have referred to the Miraflores Street site as a coldwater deposit because the otoliths represent a fish fauna such as one would find off central and northern California today (Fig. 31). A deposit such as this could reflect from one to 1,000 years or more of geological history, and within such a period many temperature anomalies could have occurred. If ocean temperatures had fluctuated widely, an admixture of "northern" and "southern" species should have resulted. Radovich (1961) showed that widespread changes in ocean temperature will result in a temporary displacement or redistribution of marine animals beyond their normal range. When such conditions exist for lengthy periods, breeding communities often become established, at least among the vertebrates. Fast-moving organisms (e.g., fishes) can also reflect short-duration temperature anomalies wherein both "northern" and "southern" species invade an area almost simultaneously (Fitch, 1966a). The lack of remains from southern fishes in this deposit indicates conditions were relatively stable during the period of deposition (i.e., there was no intrusion of warm water), or if oceanic warming did occur, very few fishes took advantage of it.

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during his diving activities. My deepest appreciation goes to my wife, Arline, whose constant encouragement and helpful advice are always uncomplainingly available, even after weeks-on-end when she is unable to use the dining room table for its intended purpose because it is piled high with microscope, dirt samples, vials of otoliths and other fish remains, references, manuscripts, and similar miscellany which are vital in this work.

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# ASPECTS OF THE BIOLOGY OF THE LIZARDS OF THE WHITE SANDS, NEW MEXICO

*By* JAMES R. DIXON

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# ASPECTS OF THE BIOLOGY OF THE LIZARDS OF THE WHITE SANDS, NEW MEXICO

*By* James R. Dixon[1]

Abstract: On the White Sands diurnal cycles of *Uta, Sceloporus* and *Holbrookia* involved two daily activity periods, the first between 9 to 11 AM, the second 3 to 5 PM. *Cnemidophorus* have one diurnal activity period, 9 to 12 AM. *Holbrookia* and *Sceloporus* appear to have similar reproductive cycles and produce one egg clutch each season, while *Uta* produces at least two egg clutches during the same period. *Cnemidophorus* seems to have a long incubation period, with only one egg clutch each season. *Uta* and *Sceloporus* appear to maintain a body temperature between 34 to 36°C, *Holbrookia* between 35 to 39°C, and *Cnemidophorus* between 37 to 39°C. The *Holbrookia* population appears to have diverged most significantly from the parental stock, followed by *Cnemidophorus, Sceloporus,* and *Uta.*

## Introduction

The White Sands of New Mexico are located in the south central part of the state, approximately 88 kilometers northeast of Las Cruces and 24 kilometers west-southwest of Alamogordo, on U.S. Highway 70-82. The sands represent a large, uniform environment, probably of pre-Pleistocene origin, and support several endemic plants, invertebrates, and vertebrates. Most of the populations on the dunes differ strikingly in color from allied populations from immediately adjacent situations and offer an interesting natural experiment in speciation.

The organisms inhabiting the white sands have been studied by many people, notably Benson (1933), mammals; Bugbee (1942), invertebrates; Emerson (1935), plants; and Smith (1943), Lowe and Norris (1956), Ruthven (1907), reptiles. However, no one has attempted to study the lizards in their natural environment except Dr. Charles H. Lowe, Jr., and party in the late 1940's and early 1950's (Lowe, pers. comm.). The present study was initiated in June 1963, and was continued during the summer months of 1964 and 1965. The extreme heat, absence of shade, and frequent spring wind storms made field work difficult, and efforts to maintain a daytime vigil over certain study areas within the white sands was almost impossible, particularly in areas of adobe soil.

Three species of lizards occur abundantly on the dunes, and the food habits of these forms were discussed by Dixon and Medica (1966), and no mention of food preferences is made in the present paper. Lizards were cap-

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tured either by hand or killed by a 22 caliber dust shot. All temperature data were obtained with a Schultheis thermometer, calibrated from 0 to 50°C. A total of 440 lizard's temperatures was taken.

## GEOLOGICAL HISTORY OF BASIN

Herrick (1904) gives an accurate account of the geologic history of the basin and provides several interesting hypotheses involving its past.

The essence of Herrick's paper is that intensive faulting in late Cretaceous or early Tertiary reduced the Tularosa Basin to its present level, though some dislocations may have occurred at a later date. He believes that a river of considerable magnitude occupied the valley and flowed southwestward to enter the Rio Grande Valley (and river) in the vicinity of El Paso. This ancient river was later diverted, probably westward, by a great sheet of "mal pais" introduced by basaltic overflows in the Tertiary. This large lava mass essentially cut off the flow of water from the north end of the basin and blocked it completely. A long period of periodic rainfall and intermittent aridity assisted in silting up the outlet towards El Paso, forming a large ancient lake that is now recognized as Lake Lucero.

Herrick estimated the size of the ancient lake as 1600 to 1800 square miles. The old shore lines are now buried under the talus from the mountains. Some of the talus deposits are 800 feet thick at the present time. Erosion has exposed the remnants of old lake benches along the northwest border of the basin and these are considered the early margins of the lake.

The present lake bed has been examined to a depth of 200 feet, and consists of successional layers of gypsum and saline beds intercalated in gypsiferous marls. The San Andres Mountains to the west and the Sacramento Mountains to the east are layered with Cretaceous sandstone and shale, and with Permian soft gypsiferous shales and sandstones. Weathering of the layers has probably produced the present sediments occupying the lake bed. The majority of the springs that feed the basin are only a few hundred yards long in most cases, and are high in dissolved salt content. Mal Pais Spring contains 15 per cent dissolved salt, Salt Creek 35 per cent, Lost River 7 per cent, and the Tularosa River 7.8 per cent.

At the present time, as in the historic past, percolating water from summer rains and melting winter snow carries tons of dissolved gypsum and salt from the mountains into the lake bed. The warm spring and summer winds evaporate the water and deposit extensive beds of pure gypsum on the surface. The wind picks up the gypsum particles and deposits them to the northeast, the direction of the prevailing winds. These deposits have formed extensive dunes that are now under the jurisdiction of the U. S. Park Service, the White Sands National Monument.

The white sand dunes are continually changing their shape and moving to the northeast at the rate of a few centimeters a year. The older dunes lying

to the southwest have become stabilized with vegetation. These dunes are now encrusted with a mixture of adobe soils and gypsum. The present active dunes occupy some 444 square kilometers of the basin, and may rise as high as 10 meters from the basin floor. They are composed of almost pure gypsum (hydrous calcium sulphate) and are generally damp within a few centimeters of the surface. The water table is high most of the year, usually within one meter of the surface of the depressions that lie between the dunes.

## VEGETATION AND CLIMATE

The adobe soils surrounding the dunes support 13 species of grasses, the common ones being three awn (*Aristida* spp.), drop seed (*Sporobolus* sp.), muhly (*Muhlenbergia* sp.), gramma (*Bouteloua* sp.), alkali (*Distichlis* sp.), burrograss (*Scleropogon* sp.), and sand bunchgrass (*Oryzopsis* sp.). Some of the larger trees and shrubs are cottonwood (*Populus wislizeni*), mesquite (*Prosopis glandulosa*), creosote bush (*Larrea tridentata*), squawbush (*Rhus trilobata*), rabbitbush (*Chrysothamnus pulchellus*), saltbush (*Atriplex canescens*), and shrubby pennyroyal (*Poliomintha incana*). The old stabilized dunes that lie to the southwest are slowly being covered by the latter vegetation (Fig. 1). A large alkali flat lies to the west of the major dune area and is essentially void of vegetation with the exception of two genera, burroweed (*Allenrolfea occidentalis*) and sand verbena (*Abronia augustifolia*).

*Figure 1.* View of stabilized gypsum dunes along the southwest edge of the White Sands National Monument. Some of the reptiles found in this area are: *Cnemidophorus inornatus, Cnemidophorus neomexicanus, Crotaphytus collaris, Sceloporus undulatus, Sceloporus magister, Phrynosoma modestum, Phrynosoma cornutum, Uta stansburiana, Crotalus atrox, Crotalus viridis,* and *Pituophis melanoleucus.*

The southern edge of the dunes is slowly becoming stabilized and one may find several stages of plant succession taking place. Some of the more conspicuous plants are *Atriplex, Rhus, Chrysothamnus,* and *Populus.*

*Figure 2.* View of the central area of the White Sands looking northwest. The arrow points to a single cottonwood protruding from the top of a dune. The depression between the dunes on the left is almost void of vegetation while the depression in the center contains a fair amount of plant cover.

The active dunes are lacking in vegetative cover with the exception of an occasional yucca (*Yucca elata*) and cottonwood (*P. wislizeni*) rising from the top of a dune (Fig. 2). The depressions between the dunes frequently have a scattering cover of sand verbena (*Phyla incisa*), primrose (*Anogra gypsophila*), sand bunchgrass (*O. hymenoides*), mormon tea (*Ephedra torreyana*), drop seed (*Sporobolus* sp.), four o'clock (*Abronia angustifolia*), yucca (*Y. elata*), and rabbitbush (*C. pulchellus*). The depressions closest to the edge of the dunes have dense vegetative cover, while those near the center of the dunes are sparse (Fig. 3). An excellent account of the plants of the white sands is given by Emerson (1935).

The average summer (June, July, August) air temperature of the dunes (six feet above the ground) ranges from 16°C at night to 38°C during the day. The average winter (December, January, February) air temperatures are 11°C during the day and −6°C at night. The summer temperatures of the adobe and gypsum soils vary with the amount of wind, moisture, and cloud cover. However, the adobe soil is generally warmer than the gypsum soils (Fig. 4).

*Figure 3*. View of a depression between the dunes in the center of the White Sands. The dark plant in the foreground is sand verbena, the scattered clumps of grass are single stands of sand bunchgrass, and the large plants in the background are *Ephedra* (mormon tea) and rabbitbush.

## NATURAL HISTORY OF THE LIZARDS

*Sceloporus undulatus:* The western fence lizard is common in the depressions between the dunes wherever rabbitbush, yucca, mormon tea, and sand bunchgrass are present. The light color phase of this species found in the center of the active dune area is occasionally found along the edgs of the dunes in adobe soil. However, none was found farther than 10 meters away from a gypsum dune. The normal dark phase found on the adobe soil is present in the stabilized dunes where the dunes have become encrusted with adobe dust. They have also been found in adobe depressions within the gypsum dunes. The latter areas have recently been captured by the movement of the dunes to the northeast, but have not become completely covered by the sand.

These lizards are never found more than a meter or two from plant cover. The majority of individuals were taken from the basal areas of rabbitbush, yucca, sand bunchgrass, or from the lower branches of rabbitbush and mormon tea. The lizards were reluctant to leave plant cover, even when pursued by hand.

There are usually twice as many males as females present at all times during June, July, and August. Both sexes are active from about 8 AM to 6 PM

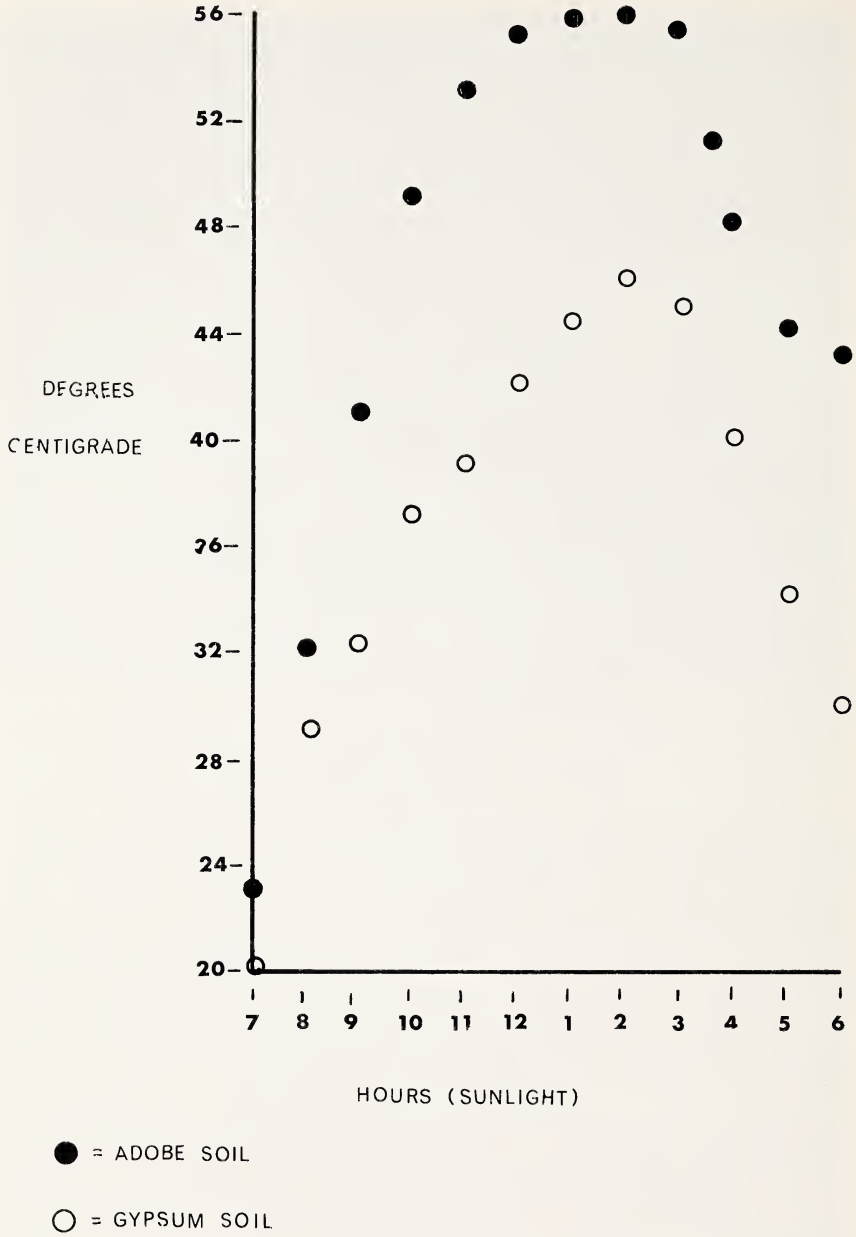



*Figure 4.* Typical daytime adobe and gypsum soil temperatures during mid-July, vicinity of White Sands National Monument headquarters, New Mexico.

on a normal sunny day. The majority of individuals were observed between 9 and 11 AM, the least number at 7 AM and 2 PM. There appeared to be a late period of activity between 4 and 6 PM (Fig. 5). The latter activity appears to be correlated to the heat holding capacity of the sand beneath dense clumps of rabbitbush. The surrounding soil temperature was 28°C while that below the shrubs was 35°C at 5:30 PM.

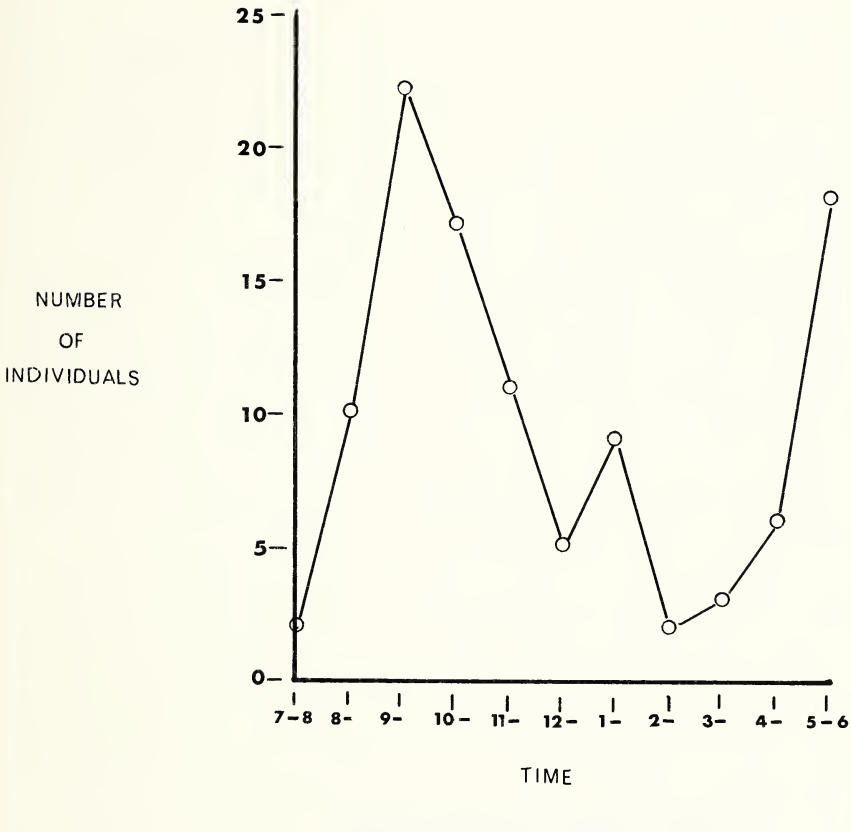



*Figure 5.* Vertical axis represents the average number of individuals of *Sceloporus undulatus* observed each hour on the White Sands during the summer months of 1963-65, horizontal axis indicates hourly intervals during the same period.

Gravid females were taken from June 12 through July 16. A few hatchlings were observed on August 16, and became increasingly more abundant in the population during late August and early September. Gravid females dis-

played bright colors on the dorsum and tail. The mid-dorsal and lateral light stripes became progressively more yellow to yellowish-orange from late June to mid-July. Shortly after egg deposition, the colors faded back to their normal gray to light buff color. This color change may be attributed to the presence of fat deposits during pregnancy and/or to a hormonal mechanism that is induced while the females are carrying the eggs. These bright colors may also tend to warn the males that the female is gravid and copulation has already been achieved.

Body temperature and associated soil and air temperatures were taken for 140 individuals during June, July, and August. The lizards were either captured by hand or shot. An analysis of cloacal temperatures resulting from the two capture methods indicated that there was no significant difference between the two methods. The body temperature was found to be higher than the ambient temperatures, except during the hottest part of the day (2 to 4 PM). The body temperature varied from 32.3°C to 37.2°C between the hours of 8 AM and 6 PM. The majority of individuals were observed sunning themselves between the hours of 9 and 11 AM. During the latter hours, the lizards were reluctant to leave their basking site when disturbed. The basking site was usually beneath the branches of plants that allowed some sunlight to filter through to the soil. From about 12 noon to 4 PM, the lizards were somewhat inactive, remaining in the shade of plant cover (Fig. 6), at which time their body temperature varied from 33.0°C to 34.7°C. The corresponding ambient temperatures indicated an appreciable drop in temperature from sunlight to shade (Fig. 6) between 12 noon and 1 PM, followed by a steadily increasing temperature towards the hottest part of the day. The lizards were again active in and out of sunlight between the hours of 4 to 5 PM.

Three individuals were captured, marked with paint, and then removed from their home site for a distance of 600 meters. The place of release was three dunes and two depressions to the northeast of the homesite, a rabbitbush flagged with red cloth. All three lizards returned to their homesite within four days, one returned in three days, the other two in four. These lizards were observed to have a small home range within the dunes, seldom moving more than 10 meters from a particular plant. The experiment, although tried only once seems to indicate that these lizards have a decided tendency to remain within familiar cover, and have some powers of orientation.

The *Sceloporus undulatus cowlesi* population occupying the center of the gypsum dunes is distinguishable from *S. u. consobrinus* populations off the dune area only by color. Lowe and Norris (1956) indicated that the two populations were distinct from one another on the basis of color, color pattern, and amount of prefrontal contact. An examination of 15 specimens from the adjacent adobe soils, 15 from the edge of the gypsum dunes, and 85 from the center of the gypsum dunes reveals evidence of gene flow between the three samples. A comparison of the number of femoral pore series, and the width

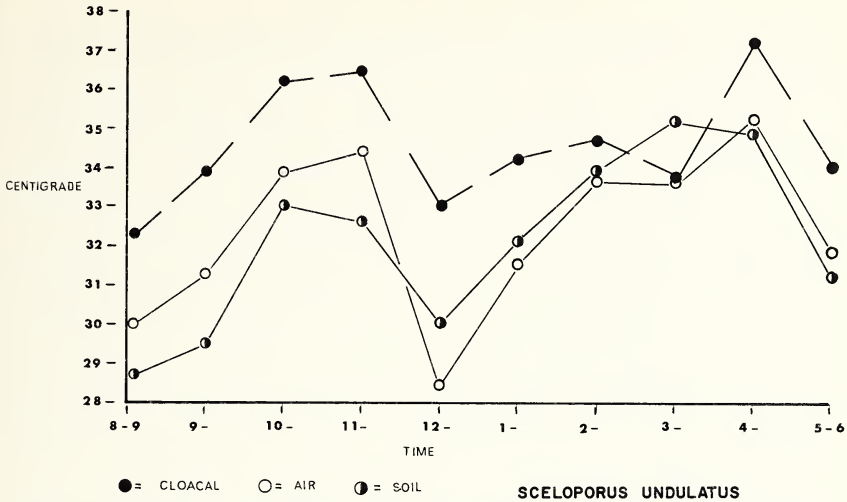



*Figure 6.* Vertical axis represents the average cloacal and ambient temperatures of *Sceloporus undulatus* on the White Sands during the summer months of 1963 to 1965, horizontal axis indicates hourly intervals during the same period. The drop in cloacal temperature between the hours of 12 and 2 indicates a period of inactivity in the shade of vegetation. The rise in cloacal temperature between the hours of 4 and 5 indicates a period of activity and basking prior to burrowing in the sand for the night.

of the mid-dorsal stripe are nearly identical in all three samples. The number of scales separating the lateral blue belly patches is ontogenetic, varying from 6 to 7 scales in specimens measuring 28 to 40 millimeters in snout-vent length, to 1 to 4 scales in specimens measuring 50 to 61 millimeters. The prefrontals are in contact with one another in 95 per cent of a sample of 23 individuals examined by Lowe and Norris (1956) from the White Sands. The amount of prefrontal contact is 37 per cent in the sample from the center of the dunes, 44 per cent in the edge of the dunes sample, and 36 per cent in the sample from the adjacent adobe soils. The latter two samples are small (15 each), but the larger series from the center of the dunes indicates a greater amount of non-contact of the prefrontals than found by Lowe and Norris (1956).

The color and color pattern of the sample from the center of the gypsum dunes are more variable than indicated by Lowe and Norris (1956). The ground color of male *S. undulatas cowlesi* is dirty gray to pale yellowish-white, with a light blue mid-dorsal stripe from the occiput to the tail. The lateral dark stripe is buff, the ventrolateral dark stripe dark gray. The belly patches are bright blue, bordered mid-ventrally with black edges. The throat patch is similar to the belly patch in color. The whitish ground color of the belly is immaculate, lacking the gray and grayish-black flecks found in individuals from the adobe soils. The female retains the basic color pattern of individ-

uals examined from adobe soils, but the ground color is more buff, with some light orange color on the top of the head, and a mid-dorsal stripe of light bluish-gray.

The ground color of the male *S. undulatus* occupying adobe soils is dark grayish-brown with a pair of dorsolateral gray stripes bordered above by a mid-dorsal grayish-brown stripe, whose intermargins are lined with a linear series of dark brown spots. The dorsolateral light stripe is bordered below by a dark brown stripe, that is in turn bordered below by light grayish-brown stripe that is bordered below by ground color. The belly is dirty white with scattered flecks of grayish or grayish-black. The lateral belly patches are bright blue, the inner margins edged with black. The throat patch is dark blue, outlined with black and united across the throat. Females are similar in color but lack the brightness of the belly and throat patches. The latter color areas are usually smaller and lack the black borders. The striping is more pronounced in the females and in addition to the mid-dorsal stripe, a series of whitish linear spots is present along its outer margins.

Individuals from the edge of the dunes are lighter in color than the adobe soil sample, but darker than those from the center of the dunes. The general ground color is light brown to buff with a lighter mid-dorsal stripe. Individuals examined from depressions between the dunes 1, 2, 3, 5, and 7 kilometers, respectively, towards the center of the dunes from the outer edge, reveal a progressively lighter ground color, especially within the first 3 kilometers. However, an occasional, relatively dark individual is found in the center of the dunes.

There is apparently more gene exchange between normal and pallid color populations than was formerly believed. This may be due to the movement of the dunes towards the northeast, capturing fresh areas of adobe soil that include normal colored individuals. These captured areas are generally extensive and may include areas up to 0.4 square kilometers.

The captured areas slowly fill in with gypsum sand, and slowly turn from dark brown soil to white soil. Light and medium dark specimens have been observed in various color stages in the captured areas.

The behavior of this species may tend to offset the selective pressure favoring the light color. These lizards tend to stay in plant cover, and 99 per cent of the plant cover is found in the depressions between the dunes, usually upon an adobe base encrusted with a gypsum-adobe mixture. The soil is usually buff to dirty gray in these areas, offsetting the brilliant whiteness of the surrounding dunes. The majority of the specimens were found in or beneath rabbitbush, mormon tea, sand bunchgrass, or on the trunks of yucca. These plants have grayish to brown bark, suggesting a selective pressure acting on the lizard population to retain brown pigment as a means of camouflage while associated with the plant cover. This selection pressure would be working counter to selection for light colors effective for travel from plant to plant.

*Holbrookia maculata:* This arenicolous lizard is common on the dunes and in depressions between the dunes. It does not seem restricted to the immediate vicinity of plant cover as is *S. undulatus*. Several individuals were found beneath rabbitbush, mormon tea, and sand bunchgrass during the heat of the day, but their foraging activity seems to be in more open areas. Individuals could not be found in adobe soils adjacent to the gypsum dunes. The nearest known locality to the white sands of normal colored individuals is 24 kilometers south of Alamogordo. The latter area is composed of reddish quartz sand and lies some 29 airline kilometers southeast of the Monument. The population inhabiting the dunes appears to be restricted to the central dune area. None was seen within 3.2 kilometers of the edge of the dunes.

Both sexes appear to be active at the same time. However, there seemed to be a third more males present in the population during June and July, with females becoming slightly more numerous than males in August. Their greatest activity period was observed to be between 9 AM and 12 noon, when the soil temperature ranged from 32 to 36°C. [On a day to day tally, greater numbers were always observed during the latter period (Fig. 7).]

As in *S. undulatus*, there appears to be a period of inactivity between 2 and 4 PM, at which time the soil temperature reaches about 40°C. Individuals were observed burrowing in the surface sand of the dunes when the soil temperature reached 40°C. They reappeared about 4 PM when the soil temperature was approximately 38°C but dropping. Individuals remained active beneath dense clumps of rabbitbush until about 6 PM, when the soil temperature beneath the shrubs had dropped to 33°C.

Gravid females were observed in June and July, with the deposition of eggs occurring over an 8-day period, July 8 to the 16th (1963). Females revealed bright colors on the hind limbs, sides of the body, and top of the head during the last week of June. The colors began as light lemon yellow and turned progressively darker and brighter (yellow to orange) through the first week of July. The top of the head became bright yellow to orange in some females just prior to egg deposition. All females captured for obtaining body temperatures on July 16 had deposited their eggs and the bright colors of the head, body, and limbs were fading to a washed-out yellow. By July 27, the colors were no longer obvious. Hatchlings were seen for the first time on August 17, and became progressively more abundant through early September.

Body temperatures and associated ambient temperatures were obtained on 176 individuals, including all sexes and ages, during June, July, and August. The body temperature was always above that for the air and ground (Fig. 8). The majority of the body temperatures were taken when the lizards were most abundant (9 to 11 AM). Many were observed basking during the latter period. This species began seeking shade at about 11 AM, when the soil temperature reached 36 to 38°C. The lizards continued to be active in and around vegetative cover until the soil temperature reached approximately 40°C.

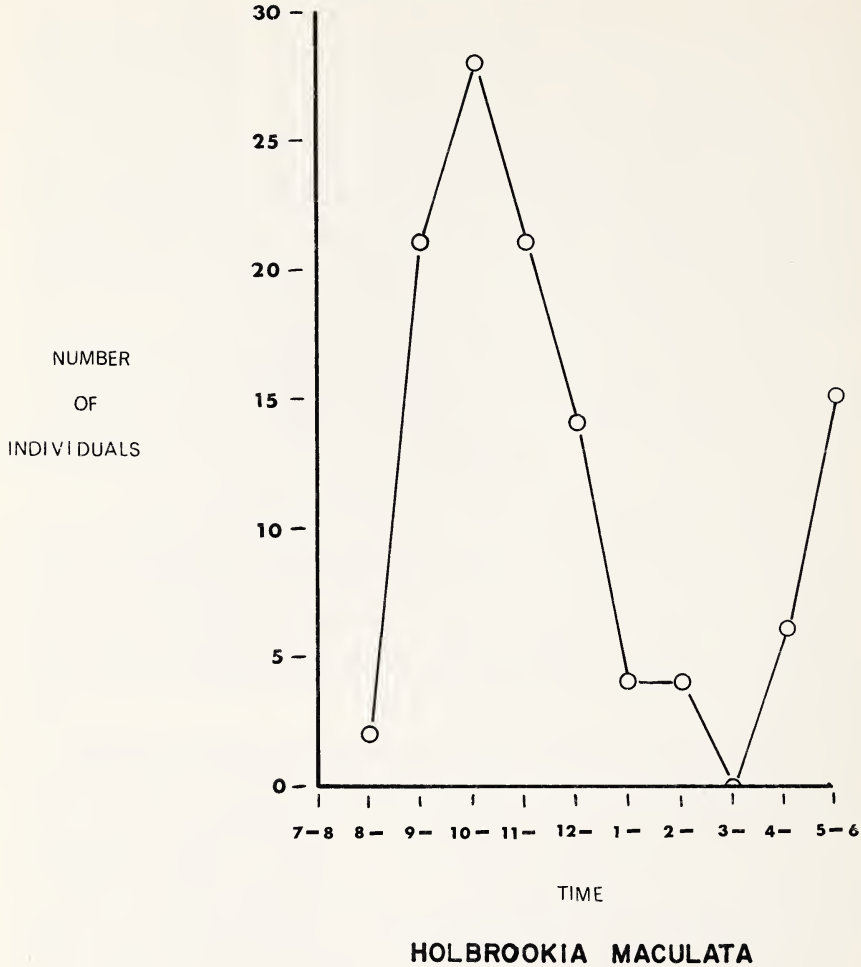



*Figure 7.* Vertical axis represents the average number of individuals of *Holbrookia maculata* observed each hour on the White Sands during the summer months of 1963 to 1965, horizontal axis indicates hourly intervals during the same period.

The white sands earless lizards, *H. m. ruthveni,* was described as a distinct form by Smith in 1943. His description of the form indicated that squamation was similar in all the samples examined, but color alone would separate the white sands form from all others (principally the closest race, *H. maculata flavilenta*).

An examination of 160 specimens from the white sands and 50 normal colored individuals from southern New Mexico indicates a much closer rela-

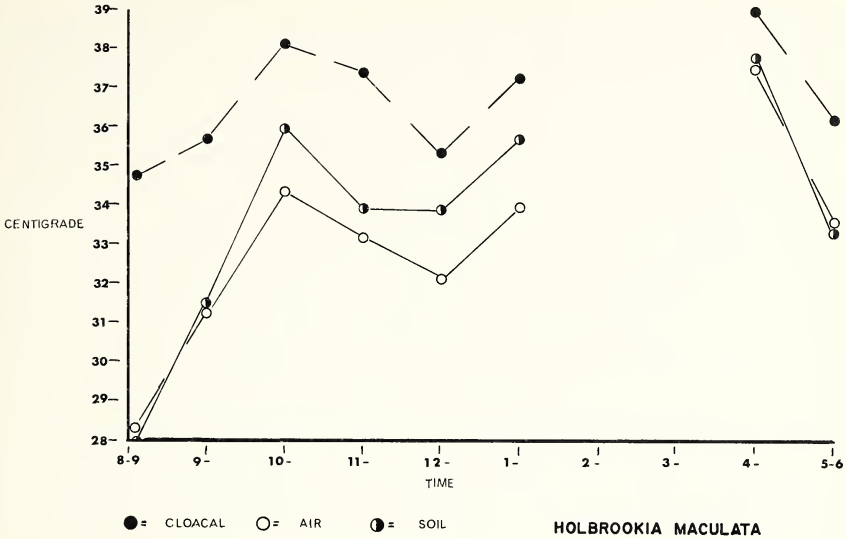



*Figure 8.* Vertical axis represents the average cloacal and ambient temperatures of *Holbrookia maculata* on the White Sands during the summer months of 1963 to 1965, horizontal axis indicates the hourly intervals during the same period. The drop in cloacal temperature between the hours of 12 and 1 indicates a period of rest in the shade. The absence of cloacal temperatures between the hours of 2 and 4 indicates the period of rest beneath the surface of the sand. The temperature between the hours of 4 and 6 indicates a period of activity prior to burrowing beneath the sand for the night.

tionship between the populations. In white sands males, the variation in ground color ranges from dark bluish-gray to light yellowish-white. A dorsal pattern of two dorsolateral linear series of small blackish spots from the rear of the head to the base of the tail is present in 90 per cent of the sample. In addition, a series of small white spots is scattered over the sides of the body, varying in intensity with the type of ground color of each specimen. The mid-dorsal area is pale bluish to bluish-white, lacking spots of any kind in most specimens. Occasionally, white spots may be present in some individuals.

Normal colored males of *H. m. flavilenta* have a ground color of light to dark brown with the dorsolateral series of black spots forming a series of chevrons that continue from the ear of the head on to the proximal one-third of the tail. The lateral white spots are present, but larger and less numerous than in the White Sands sample. The mid-dorsal area is bluish-gray to brown. The brown barring of the limbs is distinct, much less so in the white sands sample.

White sands females exhibit dorsal colors and color pattern similar to

the males, but with less white spotting. One female is almost normal colored, with distinct chevrons on the dorsum and dark flanks. The opposite extreme is also obtained, with the near absence of any dorsal pattern of any kind in some individuals.

It appears that the white sands population has retained some of the genes necessary to produce dark individuals. The majority of the samples examined were light colored, but enough darker individuals were present to cast doubt upon the validity of recognizing all white populations of lizards.

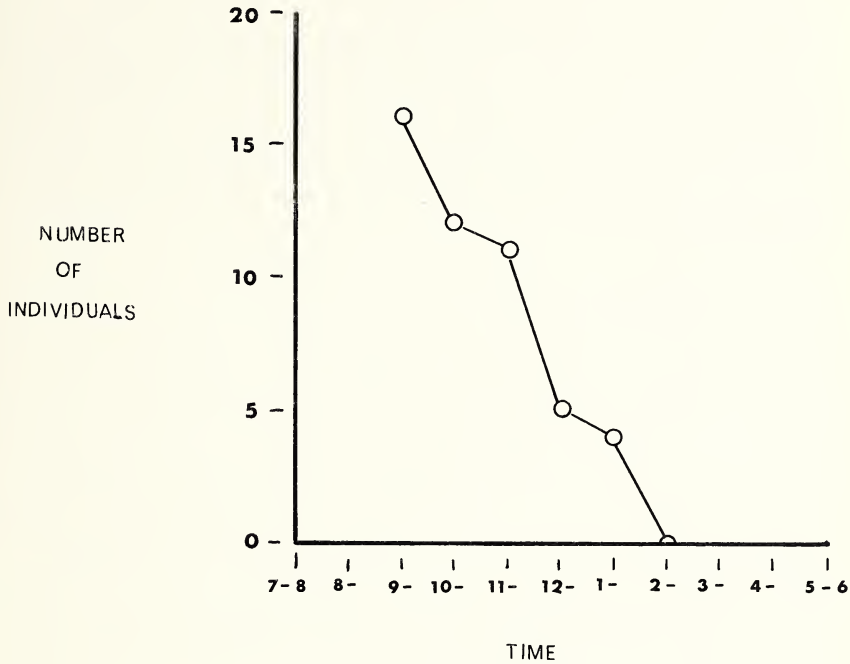
Males were observed fighting with one another on several occasions in June. Biting, tail thrashing, pursuit, and normal bluff display (see Clarke, 1965, for details of combat and display in *Holbrookia*) were used by the males. During the mid-morning period male *Holbrookia* often stationed themselves on an elevated area near the base of sand verbena or sand bunchgrass. From the latter vantage point they were observed in challenge displays. Males were seen in companionship with females on several occasions but copulation was not observed. During late morning hours males appeared to wander about more than females. The majority of females were found near vegetation during their activity periods, while males were found traversing large dunes some distance from plant cover. Usually when the tracks of *Holbrookia* were followed across the open dunes to the point where they buried themselves in the sand, the individual extracted from the sand was a male, except on one occasion.

*Cnemidophorus inornatus:* The inornate whiptail lizard is abundant throughout the depressions between the dunes, along the edge of the dunes, and was seen as far as 50 meters from the dunes in adobe soil. *C. neomexicanus* was the only other whiptail seen beyond the fringes of the dunes. The latter species also occurs in the stabilized dunes along the southwest edge of the Monument. *C. inornatus* seems to be most abundant in the depressions between the dunes where there is a considerable amount of sand bunchgrass, yucca, and rabbitbush. Low dunes that were partly covered with vegetation were frequently utilized by the lizards. A few were seen traversing the large dunes that were void of vegetation.

The sex ratio of the sample varied little over the three month summer period. Females represented 55 per cent of the sample in June, 38 per cent in July, and 45 per cent in August. Both sexes appeared to be equally active between 9 and 10 AM, with the largest numbers observed at that time. This species seldom appeared upon the surface of the white sands before 9 AM, while the population on the adjacent adobe soil was active about 8 AM. There was a definite lag (about an hour) in soil temperature between the adobe and gypsum soils during the morning hours. The adobe soil reached 33°C at approximately 8 AM, while the gypsum soil did not reach this temperature until approximately 9 AM.

As the soil temperature of the dunes reaches 33°C, the lizards become

active almost immediately. They appeared in large numbers (Fig. 9) during the first hour after their emergence from their burrows, but the numbers began to dwindle after an hour or two following their first appearance, and none was seen after 2 PM, unless the weather was extremely cool following a rain. Those individuals observed on the adobe soil disappeared at approximately 11:30 AM when the soil temperature was between 49 and 51°C.




CNEMIDOPHORUS INORNATUS

*Figure 9.* Vertical axis represents the average number of individuals of *Cnemidophorus inornatus* observed each hour on the White Sands during the summer months of 1963 to 1965, horizontal axis indicates hourly intervals during the same period.

Gravid females were observed during late June and July, but hatchlings were not seen until the latter part of August (31st). The females of this species apparently carry the eggs for a longer period of time, or the incubation period is longer. Medica (*In press*) indicated an incubation period of 46 days for *C. inornatus* from the vicinity of Las Cruces, New Mexico. In any case, the young of this species appear later during the summer than the young of *Hol-*

*brookia* and *Sceloporus*. Color change in females before and after egg deposition was not observed in this species.

Body and ambient temperatures were obtained on 84 individuals of this species. The body temperature always appeared to be 3 to 4°C above that recorded for the air and soil (Fig. 10). Most individuals were found foraging about plant cover when they were obtained for body temperatures. Most individuals were observed in direct sunlight during their foraging period, but prior to their subsequent disappearance into burrows, they were seen resting in the shade of vegetation. At the onset of the latter period, this species became very wary and sought burrows when approached. Several body temperatures were obtained from individuals while in their burrows in late afternoon. The lizard burrows were found approximately 10 to 15 centimeters below the surface at the base of sand bunchgrass, yucca, and rabbitbush. The body temperature of these lizards was approximately 2°C above that of the surrounding soil.

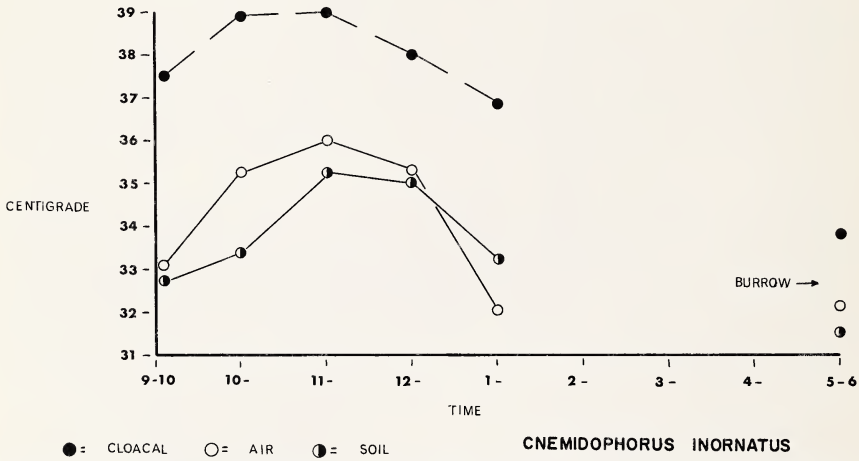



*Figure 10.* Vertical axis represents the average cloacal and ambient temperatures of *Cnemidophorus inornatus* on the White Sands during the summer months of 1963 to 1965, horizontal axis indicates hourly intervals during the same period. The absence of temperature data between the hours of 2 and 6 indicates a period of rest beneath the sand surface. The indicated burrow temperature represents 3 individuals taken from burrows on three different occasions.

The color of *C. inornatus* from the central part of the dunes is strikingly different from typical normal colored samples from southern New Mexico. The mid-dorsal light stripe is absent in about 25 per cent of the sample. The ground color is pale yellowish-gray to pale bluish-gray with the 6 to 7 light stripes present but somewhat obscure. The limbs are pale blue without a

suffusion of grayish bars on the dorsal surfaces in most specimens. The head is light brown to gray-blue in females, bright sky-blue to blue in males.

The ground color of a sample taken 20 meters from the dunes is light grayish-brown to brown, with 7 white lines distinct in all specimens. Specimens taken from the edge of the dunes are much lighter in color than those taken 20 meters into the adobe soil, but appear to be intermediate between those off the dunes and those in the center of the dunes. However, those from the edge of the dunes lack the suffused grayish bars on the upper surfaces of the limbs that are present in those on the adobe soils. A sample of 200 individuals from the vicinity of Las Cruces has a ground color of dark brown to chocolate brown with the 7 white lines greatly contrasting against the dark ground color. Two individuals of this color type were found within 50 meters of the dunes. However, an occasional individual is found in the central area of the dunes that is slightly darker than its lighter counterpart, indicating a possibility of some gene exchange with normal colored populations, or a retention of some genes for darker color.

Males were observed fighting with other males throughout the summer. In some instances the fighting pairs were not collected and sex could not be determined. The fight consisted of a bluff display, followed by pursuit, biting, and tail thrashing. Males were observed following females in July, but the females often turned and pursued the males for a short distance. Copulation was not observed in this species. Both males and females seemed to wander aimlessly over a large area. One male was followed for approximately 30 linear meters. Fighting usually occurred when the paths of two lizards crossed one another at the same time.

The majority of the burrows occupied by this species appeared to be those also occupied by the tenebrionid beetle, *Eleodes* sp. It is not known whether the beetle or lizard digs the burrow. In some instances, the burrows utilized were obviously those of *Perognathus apache gypsi.* One whiptail was found in a burrow of the pocket gopher, *Geomys arenarius.* Occasionally an individual of *S. undulatus* was found in a burrow with *C. inornatus* and tenebrionid beetles.

*Uta stansburiana:* The side-blotched lizard is common on the adobe soils surrounding the white sands, but has never been observed for more than 30 meters into the dunes. It has been taken in association with *Sceloporus undulatus*, *S. magister*, *Crotaphytus collaris*, *Cnemidorphorus neomexicanus* and *C. inornatus* on the adobe soils, and with *S. undulatus* and *C. inornatus* along the edge of the dunes. Smith (1943) indicated that *Uta* occur commonly on the dunes with *S. undulatus* and *H. maculata,* but we have been unable to find *Uta* anywhere in the dunes beyond 30 meters. Ruthven (1907) indicated that he did not find *Uta* anywhere in the white sands except on the outer edge of the dunes.

Very few *Uta* were taken in open areas between vegetative cover on the

peripheral dunes. The majority of specimens were obtained beneath the foliage of squawbush (*Rhus trilobata*) and pennyroyal (*Poliomentha incana*), both of which form dense ground cover. *Uta* were found associated with tar bush (*Flourensia* sp.), creosote bush (*Larrea tridentata*), burrograss (*Scleropogon* sp.), and gramma grass (*Bouteloua* sp.) on the adobe soils.

Both sexes were active from approximately 7 AM to 12 noon. The lizards spent the remainder of the day in dense shade and in rodent burrows. The majority of individuals were observed between 8 and 11 AM, with their numbers decreasing gradually until the soil temperature reached 50°C+ in open sunlight on adobe soils, and 40°C+ on the edge of the dunes (Fig. 11). A few sporadic observations were made on *Uta* in the afternoon on the adobe soils. The area surrounding the dunes becomes unbearably hot from noon to about 4:30 PM, making continuous observations difficult.

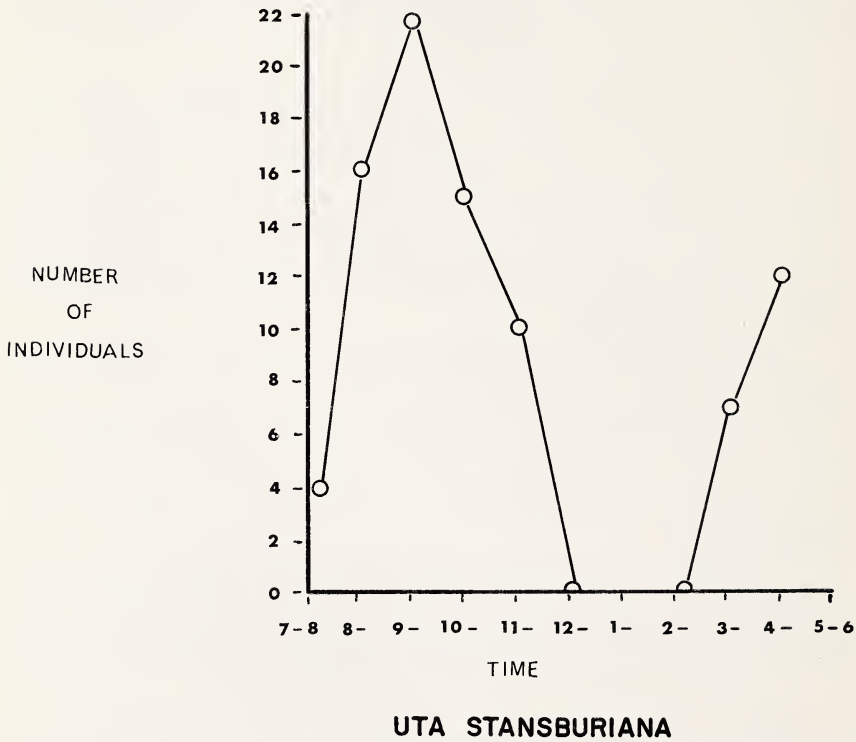



*Figure 11.* Vertical axis represents the average number of individuals of *Uta stansburiana* observed each hour along the edge of the White Sands during the summer months of 1963 to 1965, horizontal axis indicates hourly intervals during the same period. The absence of individuals between the hours of 12 and 3 is probably due to inadequate observations during this period.

Gravid females were observed in mid-June and mid-July, with hatchlings present in the population on July 23 and August 25. The latter observations lend support to Tinkle's (1961) study that mature females may have as many as three clutches of eggs per year (reproductive season).

The body temperature of 40 individuals of *Uta* from the adobe soils is higher than the air temperature, but much lower than the soil temperature (Fig. 12). The soil temperature increased at a rapid rate between 10 AM and 12 noon, and the density of *Uta* was noticeably less after the soil temperature reached 39°C. *Uta* appeared to be active on the adobe soils from 7:30 AM (soil temperature 36°C) to 10 AM (soil temperature 43°C and rising rapidly).

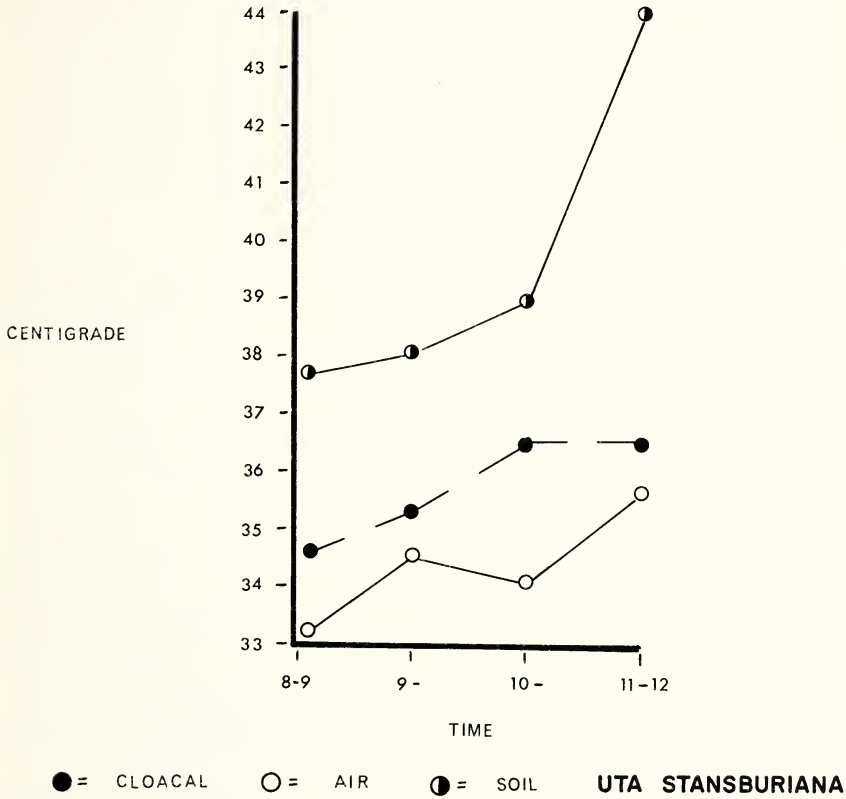



*Figure 12.* Vertical axis represents the average cloacal and ambient temperatures of *Uta stansburiana* along the edge of the White Sands during the summer months of 1963 to 1965, horizontal axis indicates hourly intervals during the same period. The absence of temperature data for the afternoon period is due to inadequate sampling during this period. Note the high soil and low cloacal temperatures during the morning hours.

They were observed feeding, basking, and presenting territorial displays during the latter period.

The ground color of individuals on the gypsum dunes and on the adobe soils is similar. The small sample from the edge of the dunes is slightly lighter in color, but the basic color and color pattern are identical to the sample obtained from the adobe soils.

## DISCUSSION

Each of the four species of lizards found within the immediate vicinity of the White Sands of New Mexico shows a distinctive evolutionary mode. Each species has adapted to the white environment in a slightly different fashion as an interaction between the forces of genetic materials and natural selection.

The dunes population of *Sceloporus undulatus* appears to have some gene flow with its parental population on the adobe soil. Individuals found along the fringes of the dunes are intermediate in color and color pattern between the dunes and adobe soil populations. Occasionally a dark individual is found well within the confines of the dunes and a light individual near the edge of the dunes on adobe soil.

The presence of dark colored individuals is probably due to the behavior of the species. *S. undulatus* is associated with dense shrubby vegetation. Selection for cryptic coloration probably favors the survival of dark individuals living in close association with vegetation. This is evident in the adobe soil population. The survival of individuals foraging for food on dark soils and traversing open areas in search of food and sexual companionship is enhanced by dark coloration. The white gypsum soil population is, in effect, being challenged by two opposing selective pressures: pressure favoring dark pigment associated with the microenvironment of conditions within the clumps of vegetation; pressure favoring light pigment, an adaption to the white soil macroenvironment. The latter selective pressure appears to be over-riding the selection for dark pigment on the dunes, but both pressures are still acting on the population. The few dark individuals present on the dunes are probably being selected against, but a behavior pattern of close association with the vegetation is apparently advantageous to the population, regardless of color. Eventually, the dunes population should reach an equilibrium, combining a minimum selection for dark color associated with the vegetation, and a maximum selection for the white macroenvironment.

Representatives of the dark soil counterpart to the gypsum dune population are seemingly able to wander into the dunes without being heavily preyed upon because of their association with the vegetation. Thus gene exchange between the dunes population and the dark soil counterpart does not seem to be greatly restricted at this time. The two populations probably represent ecological races in the sense of Grant (1963).

The dunes population of *Cnemidophorus inornatus* appears to have restricted gene exchange with the population on the adobe soil. The individuals sampled from the edge of the dunes are intermediate in color and color pattern between the dunes and adobe soil populations. This zone of intermediacy is narrow and occupies a belt of mixed adobe and gypsum soils from 1 to 10 meters in width along the edge of the dunes. The boundaries of the latter soil belt are abruptly demarcated, somewhat tan in the middle, but rapidly grading into dark brown adobe soil and white gypsum soil on either side.

The dunes population is very light colored with the dark stripes obscure in most specimens. Unlike *S. undulatus* this species requires open areas for foraging, between clumps of vegetation and on the bare slopes of the dunes. The absence of dark individuals on the gypsum soil indicates a strong selection for light pigment.

The population occupying the intermediate zone may represent a deme or a narrow zone of restricted gene flow between the parental stock and the paternal offspring. The latter is more likely because of the narrow width of the intermediate zone and the close proximity of light and dark individuals on either side of the zone. The two totally different environments probably enforce the restriction of gene flow at the present time and allow only intermediates to survive out of each clutch of eggs from a cross between dark and light colored individuals. According to Grant's (1963) classification of population systems, the two populations may represent contiguous allopatric races.

The dunes population of *Holbrookia maculata* seems to be completely isolated from its dark soil counterpart. No evidence of gene exchange between the dunes population and the population found on the reddish quartz sands near the gypsum dunes has been found. One intermediate colored individual was found in the center of the dunes. The dunes population may have reached the final stages of speciation where almost all individuals are white with an occasional darker individual appearing in a clutch as a remnant of the original gene pool. If this is the case, the white sands *Holbrookia* population may represent an allopatric semi-species as defined by Grant (1963). However, without genetic compatability studies the status of the dunes population will remain in doubt.

The evolutionary history of the *Uta stansburiana* populations from the vicinity of the White Sands is uncertain. *Uta* have not successfully invaded the dunes for an appreciable distance. *Uta* occur in the intermediate zone (adobe-gypsum soil mixture) and slightly beyond in more stabilized dunes. Three possible reasons for the absence of *Uta* in the major portion of the dunes are: (1) other species invaded first and filled the available niche, (2) *Uta* invaded the dunes along with the other species but could not maintain itself due to the absence of enough food and shelter (competition with the other species), (3) *Uta* is genetically unable to adapt to the white soil environment.

## ACKNOWLEDGMENTS

I wish to thank the personnel of the White Sands National Monument for their cooperation while the author was a collaborator for the Monument from 1963 to 1965. My heartfelt thanks go to Philip A. Medica, Walter and Joan Conley, and Mike and Judy Rubick who spent many hours toiling in the dunes with me. I thank the Society of Sigma Xi Grants-in-Aid of Research committee for funds for summer field work in the white sands during 1963 and W. Ronald Heyer, Robert J. Lavenberg, Dr. Charles H. Lowe, Jr., and Dr. Jay M. Savage for critically reading the manuscript.

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# RESULTS OF THE 1966 CHENEY EXPEDITION TO THE SAMBURU DISTRICT, KENYA. ORNITHOLOGY

*By* HERBERT FRIEDMANN AND KENNETH E. STAGER

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DOROTHY M. HALMOS
*Editor*

# RESULTS OF THE 1966 CHENEY EXPEDITION TO THE SAMBURU DISTRICT, KENYA. ORNITHOLOGY

*By* Herbert Friedmann[1] and Kenneth E. Stager[2]

Abstract: The 1966 Cheney Kenyan Expedition was organized and lead by Mr. William J. Cheney, whose primary goal was to collect a pair of leopards for an exhibition group in the Museum. The choice of locality was determined by this consideration, but as the area visited is one that has been little studied, the birds collected help to fill gaps in the distributional data on many of the included species. Some 151 species and subspecies were obtained, and are reported on in this paper.

The 1966 Cheney Expedition of the Los Angeles County Museum of Natural History worked in the Samburu District of the Northern Frontier Division of Kenya. The region was selected as a likely place in which to obtain a pair of leopards needed for an exhibition group, and of considerable interest ornithologically as well. The expedition suceeded in its chief objective, and not only assured the Museum a fine habitat group of leopards but also obtained a pair of the relatively little known aardwolf. This will give the Museum the opportunity to create a habitat display of this rare animal, a quite unexpected addition to our African exhibits.

The expedition departed from Nairobi, Kenya, on June 1, 1966, and travelled north to the Samburu District by way of Fort Hall, Nyeri, Rumuruti and Suguta Marmor. Camp was established at the west base of the Karissia Hills, approximately 10 miles southeast of Maralal, on June 1, 1966, (Fig. 1). The camp was located at Bauwa in the Lorogi forest at an elevation of 6,500 feet, and the expedition collected in this area from June 2 through June 20. On June 21 the expedition moved camp to the west base of Mt. Nyiru (Fig. 1) and collecting continued in that area from June 21 through June 27. On June 28, 1966, the expedition returned to Maralal and then on to Nairobi, arriving there on June 30, 1966.

Expedition personnel consisted of William J. Cheney, sponsor; Kenneth E. Stager, ornithologist; Peter Saw, professional hunter (Monty Brown Safaris) and his African staff of thirteen men. One trained specimen preparator was provided by Mr. John G. Williams of Nairobi.

For kindly comparing one puzzling specimen with material in the large van Someren collections in the Field Museum of Natural History, grateful acknowledgment is made to M. A. Traylor of that institution. The main acknowledgment the Museum wishes to make is to the generous sponsor and

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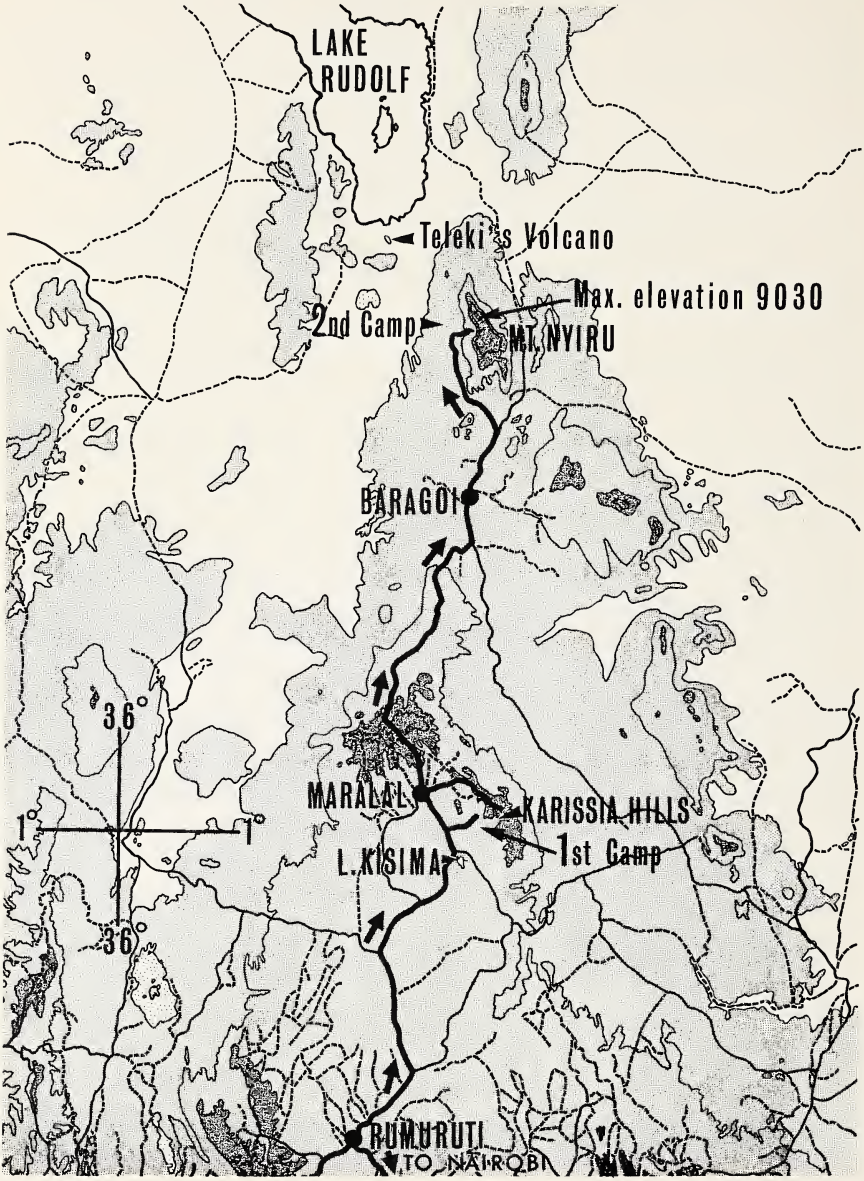


*Figure 1.* Map of the Samburu District, Kenya, showing collecting localities.

leader of the expedition, Mr. William J. Cheney, a long time friend and benefactor of the Museum. He made possible the trip, the results of which have enriched the Museum and have contributed to the advancement of our knowledge of the bird life of a seldom visited portion of eastern equatorial Africa. Mr. Cheney and his mother, Mrs. Eva Cheney, not only assumed the cost of the expedition but also provided the funds for the publication of this report on its work.

Thanks are due the Chief Game Warden of Kenya, Mr. David W. J. Brown, for the granting of the official permits necessary for the accomplishment of our goals. Special thanks are due Major R. T. Elliott, Divisional Game Warden, Northern Frontier Division, Maralal, for his hospitality and assistance to the expedition while it was working in his administrative area.

The junior author made the present collection, supplied the field notes and the photographs used in this paper. The senior author is responsible for the identifications, systematic notes, and the brief historical introduction. Each of the two authors read and approved the parts written by the other.

The present collection is the most extensive yet reported from the area, and, as such, fills in locality records for many species. As might have been anticipated, these provide no surprising extensions of known ranges, but are briefly presented in this paper as supplemental to previously published data.

The first explorers to traverse the area with which this report is concerned were the party of Count Samuel Teleki, who (1887-1888) proceeded northwards from Kilimanjaro, past Mt. Kenya, and up along the eastern side of the Rift Valley, eventually discovering Lakes Rudolf and Stefanie. The count's companion, Ludwig von Höhnel, published in 1894 a two volume narrative account of this trip, but it contains only a few casual references to the birds seen or collected. No specimen records of Teleki's or Höhnel's are extant so far as published evidence goes, if, indeed, any were collected.

In 1912 the Childs Frick expedition, with Edgar A. Mearns as chief collector, skirted the eastern edge of the area on its way south from Ethiopia to central Kenya and to Nairobi. They collected assiduously in the areas southeast of Lake Rudolf, recording 17 species in one day on the southern slopes of Mt. Nyiru (called Nyero Mts. on its labels), others at South Horr, just to the east of Mt. Nyiru, and still others in the Indunumara and Endoto Mountains; all in about 10 days in July, 1912. Its material was included in the detailed, complete report on its entire traverse of Ethiopia and Kenya, by Friedmann (1930, 1937).

One other collection, never published on and of unknown size and coverage, was made in the Samburu district in 1911-1912 by A. B. Percival, then of the Kenya game department. In all probability, Percival collected only casually while passing through the area. Jackson (1938, pp. 880, 901, 1311, 1342) lists four species of birds taken by Percival on Mt. Nyiru: *Stelgidocichla latirostris eugenia, Dioptrornis fischeri, Zosterops virens kaffensis,* and *Cin-*

*Figure 2.* Forest cover in vicinity of expedition camp at the southwest foot of the Karissia Hills, N.F.D., Kenya, June 1966.

*Figure 3.* Forest cover on the crest of the Karissia Hills, N.F.D., Kenya, June 1966.

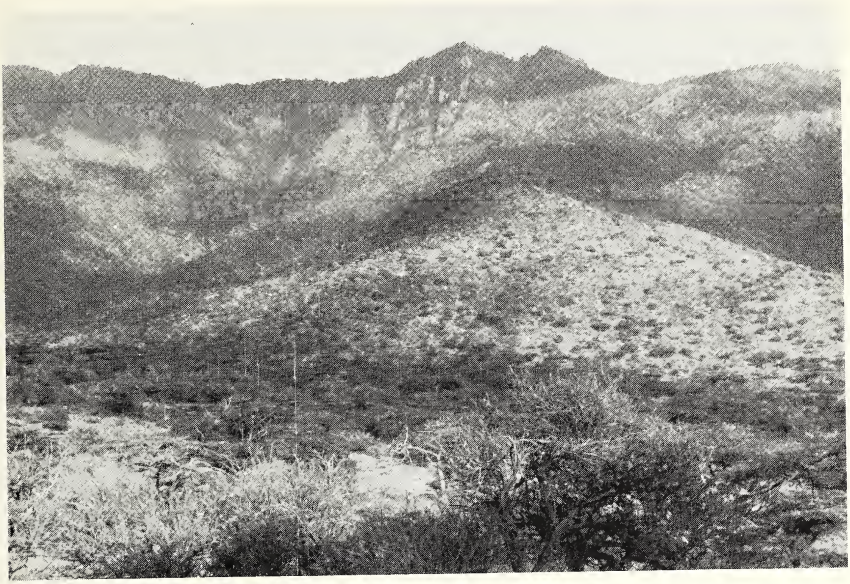

*Figure 4.* View of the west face of Mt. Nyiru from the vicinity of the expedition camp at Tum. June 1966.

*Figure 5.* View of plains area to the west from the base of Mt. Nyiru, in the vicinity of Tum. June 1966.

*nyris mediocris mediocris* (nomenclature given as in Jackson's book). Of these the bulbul and the sunbird are not represented in the present collection. *Dioptrornis fischeri* is the same as the *Malaenornis chocolatina fischeri* of this paper, and *Zosterops virens kaffensis* is probably our *Zosterops senegalensis jacksoni*.

Although much ornithological work has been done in the Mt. Kenya area and along the Northern Guaso Nyiro River, to the south of our present region, by van Someren, Lönnberg, and others, and at Marsabit to the north of it, no collections other than of casual, odd specimens appear to have been made in the Samburu District.

In our treatment of the birds collected we have followed for the most part the most recent check list of C. M. N. White as far as nomenclature is concerned. Where we have thought it called for, we have recorded taxonomic comments and observations not necessarily in complete accord with White's conclusions. In this way it is hoped that the present list may be used most easily by other students of East African birds.

## ANNOTATED LIST OF SPECIMENS

### FAMILY PODICIPEDIDAE

*Podiceps ruficollis capensis* Salvadori

The African little grebe is widely distributed from Senegal to Ethiopia, south to South Africa, wherever there are lakes or permanent streams. One adult male, with somewhat enlarged gonads, in good breeding plumage, was collected in the Karissia Hills on June 19. The locality is an addition to previously reported occurrences, but does not extend the known range of this bird. Several grebes of this species with downy young were observed on the reservoir formed by the dam across the stream at Bauwa in the Karissia Hills between June 5 and 20.

### FAMILY ARDEIDAE

*Egretta intermedia brachyrhyncha* (Brehm)

The African yellow-billed egret is represented by one specimen, an adult female, with slightly enlarged ovary, collected at Lake Kisima on June 17. This is a new, but not surprising, locality record for this bird.

### FAMILY ANATIDAE

*Alopochen aegyptiaca* (Linnaeus)

The Egyptian goose occurs throughout most of Africa. An adult male was obtained in the Karissia Hills on June 14. A common species at Bauwa in the Karissia Hills where one pair with five downy young were noted on June 15. Numerous on Lake Kisima on June 17.

*Anas sparsa leucostigma* Rüppell

The African black duck was met with in the Karissia Hills, where a male was collected on June 9. This bird is in an advanced stage of molt; it has lost all of its old remiges and the new ones are just sprouting, leaving the bird entirely incapable of flight. This duck is found chiefly in wooded streams in the uplands of Kenya, where it is apt to remain hidden in the vegetation along the banks. This causes it to seem less numerous than it probably is.

*Anas erythrorhynchus* Gmelin

The red-bill is one of the commonest of east African ducks. Three specimens in good plumage were collected as follows: Karissia Hills, June 9, one adult male; 15 miles south of Maralal, June 17, one adult of each sex.

## FAMILY ACCIPITRIDAE

*Aegypius tracheliotus* (Forster)

An adult female weighing 14 lbs. (6.36 kg.) was obtained on the open plains area, 10 miles south of Maralal, on June 9, 1966. On June 10, 1966, an adult male weighing 16 lbs. (7.26 kg.) was secured in the same general area, 15 miles south of Maralal. Neither bird showed any evidence of being in breeding condition.

It is questionable whether *Aegypius* and *Torgos* are congeneric as held by White, but for the present we will go along with this arrangement. There are many basic differences between *Torgos* and *Aegypius,* including the size and conformation of the brain.

The ratio of numbers of these large lappet-faced vultures to other vultures in the Maralal–Mt. Nyiru area was noted to be roughly one pair of the former to any large assemblage of vultures at a kill.

*Trigonoceps occipitalis* (Burchell)

Two specimens, one of each sex, of the white-headed vulture were obtained in the plains area at the south end of Mt. Nyiru, on June 23, 1966. The two are quite dissimilar, as the adult female has the large inner secondaries and broad edges on the median upper wing coverts white, while the subadult male has the inner secondaries dark silvery grayish and has largely lost the pale edges of the coverts through abrasion. Each of the above specimens weighed 10 lbs. (4.54 kg.).

This vulture is generally stated to be relatively uncommon although widely distributed throughout the drier portions of Kenya (Jackson 1938: 139; Lonnberg, 1911: 54). Sharpe (1931: 10) found it on Marsabit Mountain; Mt. Nyiru seems to be a new, if not a surprising locality for this bird.

White-headed vultures were frequently observed in the Karissia Hills–Maralal area, but no specimens were collected. The relative abundance of this species of vulture in the area was approximately one pair per gathering of

vultures at a given kill. Each time a zebra was killed for leopard bait in the Maralal area, a pair of *Trigonoceps* and a pair of *Aegypius* would join the throngs of *Gyps*.

*Gyps bengalensis africanus* Salvadori

Two specimens, representing two very different plumages, of this vulture were collected 10 miles south of Maralal, June 9, 1966, an adult female (weighing 10 lbs. or 4.54 kg.) and an immature of the same sex (7 lbs. or 3.18 kg.). In treating the African white-backed vulture as a race of the Asiatic *bengalensis* we are following White (1965: 41). This is a common vulture throughout Kenya and its occurrence near Maralal, though not previously reported, is not unexpected.

White-backed vultures are exceedingly common in the Maralal area and, combined with Ruppell's griffon, make up the bulk of the vulture population of northern Kenya. It was interesting to note that these gregarious vultures have apparently become conditioned to the food opportunities afforded by hunting safaris, as large numbers of vultures will follow above and behind a hunting vehicle heading out across the plain. When the vehicle stops, the vultures will begin circling above in soaring flight. A hunter with rifle moving out from the vehicle on foot will cause many of the circling birds to begin their descent, apparently in anticipation of immediate food.

*Gyps ruppellii rupellii* Brehm

An adult male weighing 12 lbs. (5.45 kg.) was obtained on the open plains area, 10 miles south of Maralal, on June 9, 1966.

Ruppell griffons are extremely common in the Maralal–Mt. Nyiru plains areas. Their numbers were roughly equal to those of the preceding species, *Gyps bengalensis*.

*Necrosyrtes monachus* (Temminck)

The hooded vulture is represented in the collection by an adult male taken in the Karissia Hills, June 17, 1966. It had small testes, and is in fairly abraded plumage; this is especially true of the retrices and inner greater upper wing coverts. In using a binomial for this bird we follow C. M. N. White (1965: 42), who pointed out that the change in size of these birds from the smallest West African examples to the largest East and South African ones is so gradual that it is difficult to know where, if at all, to draw a line. It is true that Mackworth-Praed and Grant (1957: 137) consider the eastern and southern birds as forming the race *pileatus,* to which the present example would belong. The hooded vulture is one of the commonest species of its group in many areas of Kenya.

Although White (1965) considers *Necrosyrtes* and *Neophron* to be congeneric, we hold that *Necrosyrtes* should be retained as a valid genus, as it differs very profoundly from the Egyptian vulture. Cranial casts of the brain

of the two genera show them to differ decidedly in shape. The external nares of *Necrosyrtes* are not nearly as large as those of *Neophron*. There are many differences in plumage texture and composition between the two forms. In *Necrosyrtes* the feathers of the occiput and nape are short and velvet-like while those of *Neophron* are narrow, elongate and pointed. The chest of *Neophron* is covered with normal contour feathers while in *Necrosyrtes* a pronounced crop patch is developed with a prominent border of white down feathers. The tail of *Neophron* has a sharply graduated tail of 14 feathers while that of *Necrosyrtes* is almost square with 12 feathers.

Hooded vultures were well represented in all large vulture gatherings in the Maralal–Mt. Nyiru plains areas and several birds were always to be found about our camp areas, in the company of tawny eagles (*Aquila rapax*). Perching in the trees about the periphery of the camps, these scavengers were always on the alert for carcasses discarded during specimen preparation.

*Neophron percnopterus percnopterus* (Linnaeus)

One adult male Egyptian vulture was obtained in the plains at the west foot of the Karissia Hills, June 12, 1966. This species is chiefly a bird of the interior highlands along the Rift Valley in Kenya. Although a common bird in many parts of East Africa, the Egyptian vulture proved to be the least common of the six species of vultures encountered in the Maralal–Karissia Hills area.

*Circaetus cinereus* Vieillot

An adult female brown harrier eagle was collected on the west base of Mt. Nyiru, June 23, 1966. It was in non-breeding state, with small ovary, and was in fairly worn plumage. Jackson (1938: 190) gave a previous record from the Samburu district, but stated that the species is rather rare in the interior of Kenya. This individual was the only *Circaetus* observed during the course of the field work. In flight the bird appeared perfectly normal, but examination of the sternum showed evidence of a previous injury that had resulted in extensive fracturing and subsequent mending of the bone tissue.

*Accipiter badius sphenurus* Rüppell

This small hawk is represented by one adult female, taken at the west base of Mt. Nyiru, June 23, 1966. The bird was in non-breeding condition, and in good plumage.

*Melierax poliopterus* Cabanis

The pale chanting goshawk was met with on June 24, on the west base of Mt. Nyiru, when one adult male and two adult females, all with small gonads, were collected. These three are definitely *poliopterus,* but the male has a very few dusky cross bars on the white upper tail coverts, suggesting a variation in the direction of the related and sympatric *M. metabates*. Similarly, one of the females shows some freckling on the inner webs of a few of the upper wing

coverts, but nothing like the degree to which this character is developed in *M. metabates*. Chanting goshawks were not met with in the Karissia Hills area, but observations were made on the harrier hawk, *Polyboroides typus*. A single individual of this species was observed in flight, vigorously pursued by large numbers of glossy starlings of several species. Disregarding the starlings, this large hawk was repeatedly observed to raid the nesting colonies of the grey-headed social weaver (*Pseudonigrita arnaudis*). The hawk was observed to grasp the nest in its talons and pull it apart by hanging upside down and beating the air with its wings. Frequent movements of the hawk's head towards the nest were made, but observations was too distant from the scene of predation to note whether or not any adult or nestling weavers were taken.

*Buteo rufofuscus augur* (Rüppell)

The augur buzzard is represented by two adult specimens, a female taken in the Karissia Hills, June 9, and a male taken 5 miles west of Maralal, June 15. Both birds were in non-breeding state, with small gonads. This is a common, widely distributed bird in the interior of Kenya and numerous individuals were observed in the Maralal area.

*Aquila rapax belisarius* (Levaillant)

Two examples of the tawny eagle were obtained, as follows: 15 miles south of Maralal, June 12, one female in the "usual" grayish tawny plumage; Karissia Hills, June 18, one adult male in the dark plumage phase. The female is in very worn plumage. As was shown in a detailed account of the plumage stages and phases of this eagle by Friedmann (1930: 58-62), the very dark birds are the oldest ones, possibly 5 or 6 years old. The present male is very dark on the head, throat, and breast; less so on the wings and upper parts of the body, but still dark, and dark tawny brown on the abdomen.

The tawny eagle is the commonest eagle in the interior of Kenya, where it is fairly well distributed. The present specimens add new, but not surprising, locality records for it. Tawny eagles proved to be great scavengers about our field camps, where they took up residence and fed on the discarded bird carcasses cast out each day. As many as eight individuals of this species were noted at one time at the Karissia Hills camp and always in the company of hooded vultures (*Necrosyrtes monachus*).

## FAMILY PHASIANIDAE

*Francolinus sephaena grantii* Hartlaub

Grant's crested francolin is a common, widely distributed bird of the open country of eastern Africa from southern Sudan and Ethiopia to central Tanzania. Two specimens were procured by the expedition, a non-breeding female in the plains area 15 miles south of Maralal, June 4, and a breeding male in the Karissia Hills, June 12.

*Francolinus leucoscepus infuscatus* (Cabanis)

The yellow-throated francolin occurs over much of the open, drier parts of eastern Africa from Ethiopia to Tanzania. A female collected 15 miles south of Maralal, June 7, and a male in the same place June 15. Both birds were in full breeding condition; the hen was marked as "laying." The male is larger and more deeply colored, with dark mahogany brown on the ventral feathers; the female has the white shaft streaks on the feathers of the upper part broader and the malar band of feathers less lined with dusky gray; otherwise the two are alike.

*Coturnix delegorguei delegorguei* Delegorgue

Two females of the wide-ranging harlequin quail were collected, one on June 7, 15 miles south of Maralal, and the other on June 11, in the Karissia Hills. Both birds had slightly enlarged ovaries; both are in fresh plumage.

## FAMILY OTIDIDAE

*Eupodotis ruficrista gindiana* Oustalet

The buff-breasted florican was met with at the west base of Mt. Nyiru, on June 25, when one female was collected. The bird had the ovary slightly enlarged. Mt. Nyiru is a new locality for this bird, and while not extending its known range, helps to fill in the still imperfect data on its occurrence.

## FAMILY BURHINIDAE

*Burhinus capensis maculosus* (Temminck)

The South African dikkop ranges from the Cape Province north to Kenya, changing in northern Kenya to a tawnier race *maculosus*. Two male specimens obtained in the Karissia Hills, June 11 and 12, belong to the race *maculosus*, which had been recorded previously from Horr, Marsabit, and other localities not too far from the Karissia Hills. Both specimens are somewhat abraded, and both were in non-breeding condition.

## FAMILY CHARADRIIDAE

*Vanellus armatus* (Burchell)

One adult male blacksmith plover was collected 15 miles south of Maralal, June 6. It is in slightly abraded plumage, and shows signs of molt in the tail, the outermost rectrices being only an inch in length and still enclosed basally in their sheaths. The bird had the testes somewhat enlarged. Maralal must be about the northern limit of the range of this plover; Jackson (1938: 355) considered it to occur only in southern Kenya, south to Natal, and gave no locality record north of Naivasha, Elmenteita, and Nakuru. Mackworth-Praed and Grant (1957: 358) wrote that in Kenya it was most abundant in the Rift Valley, and noted its breeding there from April to August. The

present specimen, judging by its plumage and by its gonadal state, was probably through breeding, and was therefore one of the early breeders.

We follow White (1965: 120) in considering the genus *Hoplopterus*, formerly used for this bird, as part of *Vanellus*.

*Vanellus coronatus coronatus* (Boddaert)

The crowned lapwing, a common bird of the fairly dry, short grass area of Kenya, was collected in two localities. On June 10 an adult male, with somewhat enlarged gonads, was taken 15 miles south of Maralal; on June 12 another male and a female with large ovarian eggs were collected in the open plains at the foot of the Karissia Hills. All three specimens are in somewhat abraded plumage. This species was formerly placed in the genus *Stephanibyx*, which White (1965: 122) later considered as part of the broader group *Vanellus*.

*Charadrius pecuarius pecuarius* Temminck

Kittlitz's sand plover is a widely distributed bird over much of Africa, in dry open places. The expedition obtained one adult male, with enlarged testes, at Lake Kisima, on June 17. The specimen is in abraded plumage.

*Charadrius tricollaris tricollaris* Vieillot

The three-banded plover is a common bird of the mud flats, beaches, and open areas near water, throughout much of Africa. It is represented in the present collection by the following three specimens: June 4, Karissia Hills, one female with slightly enlarged ovary, one male with enlarged testes; June 6, plains area 15 miles south of Maralal, one female with enlarged ovary.

## FAMILY GLAREOLIDAE

*Cursorius temminckii* Swainson

Temminck's courser is a bird of the open, short grass country throughout Kenya. On June 4, two specimens, one of each sex, were obtained in the plains area 15 miles south of Maralal; both birds were in breeding condition.

## FAMILY COLUMBIDAE

*Columba guinea guinea* Linnaeus

One adult male speckled pigeon, with considerably enlarged testes, was obtained at the west base of Mt. Nyiru on June 26. This is a bird of the open country where it goes about in small flocks. According to Peter Saw, the professional hunter with our field party, the speckled pigeon is known to form fairly large flocks in the Mt. Nyiru area where it is often sought as a game bird by hunting safaris.

*Streptopelia lugens lugens* (Rüppell)

This dark pigeon is represented by two specimens in the collection; an

immature female taken in open plains country 15 miles south of Maralal, on June 10, and a non-breeding adult male collected in the Karissia Hills, June 11. White (1965: 156) considered this pigeon to be a bird of montane forests, but the present immature female, found in open country, suggests a broader ecological range of habitat for it.

*Streptopelia semitorquata* (Rüppell)

In naming the specimens of the red-eyed dove binomially we are following White (1965: 156-157) who found the proposed races were not well enough differentiated for separate recognition. Three examples were collected by the expedition, all in the Karissia Hills, a female with small ovary on June 3, another with somewhat swollen ovary on June 14, and a male in breeding condition on June 4.

*Streptopelia senegalensis senegalensis* (Linnaeus)

The laughing dove, a widely distributed and common bird over much of Africa south of the Sahara, except in forested areas, was met with on the west base of Mt. Nyiru, where an adult male with greatly enlarged testes was collected on June 26.

*Oena capensis* (Linnaeus)

This long-tailed little dove is represented by one specimen, an adult female with slightly enlarged ovary, taken at Lake Kisima on June 17.

*Turtur tympanistria* (Temminck)

The tambourine dove occurs throughout Kenya in wooded areas. The expedition obtained an adult male in breeding condition in the Karissia Hills on June 10. We follow White (1965: 161) in treating this bird binomially.

*Turtur chalcospilos* (Wagler)

The emerald spotted dove is a woodland bird of very wide distribution in Africa. Three specimens were obtained, as follows: Karissia Hills, June 8, one adult male with enlarged testes; west base of Mt. Nyiru, June 22, one adult of each sex with somewhat enlarged gonads.

## FAMILY MUSOPHAGIDAE

*Tauraco hartlaubi* (Fischer and Reichenow)

Hartlaub's turaco is a bird of the highland forests of central and southern Kenya, eastern Uganda, and northern Tanzania. It has been found as far north as Marsabit Mountain (Sharpe, 1931: 99). Judging by the fact that the expedition obtained six specimens in the Karissia Hills, June 2 to 14, the bird must be as common there as it is on Marsabit and on Mt. Elgon. Five of the specimens are females, none in breeding condition and one of them a young bird, and the remaining one is an adult male with somewhat enlarged testes.

Turacos with a call similar to that of *T. hartlaubi* were heard on the steep, heavily-forested slopes of Mt. Nyiru, but no specimens were secured.

*Corythaixoides leucogaster* (Rüppell)

The white-breasted go-away-bird is a denizen of the open, semi-arid plains and scrub country of Kenya. On the west base of Mt. Nyiru, June 21 to 25, a series of 3 adult males and 2 adult females was collected. Some of them showed gonadal enlargement while others did not. A common species in the area about our Mt. Nyiru camp.

## FAMILY CUCULIDAE

*Cuculus solitarius solitarius* Stephens

The red-chested cuckoo was met with in the Karissia Hills, where a non-breeding female was taken on June 12 and a male, with slight gonadal enlargement, on June 15. The female shows signs of active molt in the remiges, and has many worn feathers on the upperparts; the male shows no sign of ecdysis.

Pitman (1964: 140) recorded an egg of this cuckoo taken at Baragoi, about 50 miles north of the Karissia Hills, on December 20.

*Cuculus clamosus clamosus* Latham

The name of the black cuckoo is once more *clamosus* since *cafer* Lichtenstein has ruled a *nomen rejectum* by the International Commission on Zoological Nomenclature. The expedition collected an adult male, with some testicular enlargement, in the Karissia Hills, June 19. The fact that this bird, not a breeder but also not a migrant, judging by its testes, was collected at the same place and within a fortnight of the specimens of the next form, adds to, rather than clarifies the puzzling nature of the inter-relations of these cuckoos. This specimen has one very worn outer rectrix, apparently left over from an earlier plumage.

*Cuculus clamosus gabonensis* Lafresnaye

White (1965: 184) has combined *jacksoni* and *mabirae* with *gabonensis,* and we call our specimens by the last name to conform with his check list. However, it is not yet clear whether this is the correct solution of a puzzling series of bird plumages. The detailed discussion in earlier studies (Friedmann, 1930: 263-266; Chapin, 1939: 192) and the uncertainty expressed by Jackson (1938: 488-489) make it advisable to point out that if further study with additional specimen data should necessitate rearranging the birds presently grouped together as *gabonensis,* and should reinstate some of the races, formerly recognized, our present examples would be *jacksoni.* They lack the pale ground color on the abdomen found in typical *gabonensis* and *mabirae.* Three examples, all males, and all like the type of *jacksoni,* were obtained on June 3 in the Karissia Hills. All had small testes and all are fairly similar, although

varying in the darkness of the ventral barrings and in the width of the white bars on the under tail coverts.

*Chrysococcyx cupreus cupreus* (Shaw)

The yellow-bellied emerald cuckoo occurs, chiefly in forest but also in scrub, country, throughout eastern Africa. Two adult males, both with somewhat enlarged gonads, were collected in the Karissia Hills on June 15. The Karissia Hills are a new, but hardly surprising, locality record for this bird. We are following White (1965: 187) in considering *sharpei* a synonym of *cupreus,* although his action is subject to reconsideration, as the majority of previous authors considered the two distinct.

*Centropus superciliosus superciliosus* Hemprich and Ehrenberg

One adult female white-browed coucal was obtained at Pali Pali Hill, south of Karatina, June 1, when it was hit by the car. This terrestrial cuckoo is a common and widely distributed bird over much of Kenya. The above mentioned specimen was secured enroute to the Samburu district, but the species was not encountered in either of our collecting areas.

## FAMILY STRIGIDAE

*Bubo lacteus* (Temminck)

Verreaux's eagle owl is represented in the collection by an adult female, taken in the Karissia Hills, on June 2. Its stomach contents showed it had been feeding on large coleoptera, a strange diet for so large an owl. Other observers have recorded snakes and lizards, but also caterpillars as parts of its usual food. The Karissia Hills adds a new "station" for this large owl. The above mentioned specimen was one bird of a pair that roosted in the large fever trees in the immediate vicinity of the Karissia camp.

## FAMILY CAPRIMULGIDAE

*Caprimulgus frenatus* Salvadori

White (1965: 204) treated *frenatus* as a full species and not as a race of *pectoralis,* and we are here following his decision. Two specimens are referred to this nightjar, an adult "female" taken in the Karissia Hills, June 12, and another female in the same place on June 4. The first specimen may be wrongly sexed, as it has the large remigial spots pure white, untouched with buffy, and has very broad white terminal areas on the outer rectrices. The other specimen has the remigial spots tinged with rusty buff and has no white tips to the rectrices, the terminal portions of which feathers are grayish sandy buff mottled and blurred with fuscous. The bird assumed to be a male agrees very closely with an undoubted male from "Mile 40" on the Nairobi–Magadi Road; the other fits very well with a female from Nairobi but has the terminal area of

the outermost pair of rectrices more clouded and mottled with fuscous, less plain sandy buff than the Nairobi bird. The descriptions of the female plumage given by Mackworth-Praed and Grant (1957: 667) and by Jackson (1938: 651) do not fit the present female, as they state that the terminal white tail areas are present in both sexes; but in this they seem to be in error. The specimen with the large white tail marks, our probable male, is molting in the wings, as two of the remiges of the left wing are very short and basally are still enclosed in their sheaths from which they are expanding terminally.

### FAMILY APODIDAE

*Apus niansae niansae* (Reichenow)

Two specimens of this swift were collected at the west base of Mt. Nyiru, June 24, one of each sex. They agree with a series from Mt. Moroto, northeastern Uganda, and from Naivasha, Kenya. The above specimens were shot on the wing in the late afternoon when large numbers of swifts, presumably of this species, were feeding over the scrub forest at the west base to Mt. Nyiru.

### FAMILY COLIIDAE

*Colius striatus kikuyuensis* van Someren

The speckled mousebird is one of the commonest birds of most of Africa; the present subspecies ranges from northern Tanzania north at least to Marsabit. In the Karissia Hills, June 2 and 3, a series of 4 males and 2 females was collected, all but 2 of which were marked as in breeding condition. Mousebirds of this species were exceedingly abundant in the Karissia Hills, but were absent in the Mt. Nyiru area, being replaced by the following species.

*Colius macrourus pulcher* Neumann

Two male blue-naped mousebirds were collected on the west base of Mt. Nyiru, June 26. Both had the gonads somewhat enlarged; one of the birds lacks the long rectrices, probably due to the shot. Mt. Nyiru appears to be an additional locality for this bird. Mousebirds were noted as relatively uncommon in the Mt. Nyiru area.

### FAMILY TROGONIDAE

*Apaloderma narina narina* (Stephens)

Narina's trogon is a bird of the evergreen forest throughout much of eastern Africa, but its range is discontinuous because of the spotty distribution of suitable habitat. The expedition found it to be common in the Karissia Hills, where 5 male specimens were obtained between June 6 and 12. All the birds showed gonadal swelling. All of the above mentioned birds were located by their characteristic calls and no females were seen.

### FAMILY ALCEDINIDAE

*Halcyon chelicuti chelicuti* (Stanley)

This is one of the wide-ranging, common kingfishers of the open country of Africa. One adult female was obtained on June 7, 15 miles south of Maralal; the bird was in non-breeding condition.

*Halcyon leucocephala leucocephala* (Muller)

The gray-headed kingfisher occurs over much of Africa except in treeless areas. The expedition met with it on the west base of Mt. Nyiru, where one male with somewhat enlarged gonads was collected on June 23, and one non-breeding female on June 26.

### FAMILY MEROPIDAE

*Merops pusillus meridionalis* (Sharpe)

This is one of the ubiquitous birds of the open country of eastern Africa. In the plains area 15 miles south of Maralal the expedition collected one adult female on June 4. It showed slight gonadal development. We follow White (1965: 232) in merging the genus *Melittophagus* with *Merops*.

*Merops lafresnayei oreobates* (Sharpe)

The cinnamon-chested bee-eater is a bird of the bush country of Kenya, usually at altitudes of from 6000 to 8000 feet. It was common in the Karissia Hills where the expedition collected 2 adult males and 2 immature birds of each sex, on June 14 and 15. In the Karissia Hills this bee-eater was encountered only in heavy forest where it perched in numbers on the tops of large cedars along a stream course.

### FAMILY CORACIIDAE

*Coracias caudata caudata* Linnaeus

The lilac-breasted roller was met with in the open plains 15 miles south of Maralal on June 7 and 10, on each of which days one male was obtained. With the deep lilac color extending well down over the breast, these specimens are clearly typical *caudata* and show no variation in the direction of *lorti* of Ethiopia and northeastern Kenya, in which race that color is restricted to the chin and throat.

*Coracias naevia naevia* Daudin

The rufous-crowned roller is represented in the collection by an adult male taken on the west base of Mt. Nyiru, June 26. It had the testes slightly enlarged, and is in somewhat abraded plumage. This species is widely distributed over much of eastern Africa; Mt. Nyiru is an additional, but not surprising, "station" for it.

*Eurystomus glaucurus afer* (Latham)

The broad-billed roller is found over a good part of eastern Africa. One adult female specimen was collected in the Karissia Hills, on June 2. It was in non-breeding state.

FAMILY UPUPIDAE

*Phoeniculus granti* (Neumann)

In calling our single, youngish, specimen *P. granti,* and not *P. purpureus granti,* we are conforming to the arrangement given by White (1965: 241). The present bird, a young male, taken in the plains area 15 miles south of Maralal, June 7, has the chin and throat dusky grayish fawn, and the black bill somewhat shorter (25 mm.) than birds in full adult plumage.

*Phoeniculus bollei jacksoni* (Sharpe)

This race of the white-headed kakelaar occurs in the highlands of Kenya west to the eastern Congo and north to the southern Sudan. The expedition obtained 5 male specimens in the Karissia Hills, June 2 to 12. Of these, 3 showed no signs of gonadal enlargement, one showed slight signs of it, and the last had no comment on its label.

*Phoeniculus minor cabanisi* (Defilippi)

This smallish kakelaar is a bird of the dry open country. The expedition collected one non-breeding male on the west base of Mt. Nyiru, on June 22. We follow White (1965: 243) in combining the genus *Rhinopomastus* with the broader *Phoeniculus.*

FAMILY BUCEROTIDAE

*Tockus erythrorhynchus erythrorhynchus* (Temminck)

The red-billed hornbill has a wide range in the thorn bush country of Africa. The expedition collected 4 specimens on the west base of Mt. Nyiru, June 21 to 25; 2 adult males with somewhat enlarged testes, one female in non-breeding state, and 1 immature female. All the birds show signs of molt, especially in the tail, and all have some faded old feathers still present in the upperparts.

*Tockus deckeni* (Cabanis)

Von der Decken's hornbill is represented in the collection by a single non-breeding female collected on the west base of Mt. Nyiru on June 25. The rectrices are not yet fully grown and are still enclosed in their sheaths basally.

*Tockus jacksoni* O. Grant

Jackson's hornbill is not listed in White's 1965 check list, and it is to be assumed that he considered it the same as *deckeni.* One immature female was collected on the west base of Mt. Nyiru on June 25, apparently together with

the specimen of *deckeni* listed above. However, this bird has numerous conspicuous white spots on the upper wing coverts, which are absent in the otherwise very similar *deckeni*. The discussion of these two remarkably similar, sympatric species given in an earlier study (Friedmann, 1930, 420-425) still seems to be the most informative appraisal of them, and we prefer to follow the conclusions there reached, and since accepted by Mackworth-Praed and Grant (1957: 621).

*Tockus flavirostris flavirostris* (Rüppell)

The yellow-billed hornbill occurs widely in the acacia savannas of Kenya. Three examples were obtained by the expedition on the west base of Mt. Nyiru, on June 25, 2 males and 1 female, all with somewhat enlarged gonads. Both of the males show signs of active molt in the remiges. An adult male was observed actively feeding a nesting female in a dead snag in the center of our camp area. The bird would feed the sealed-in female several times a day and the food items were often noted as large green mantids. A young fledgling of this species was purchased alive from a Samburu warrior on June 26 at the Mt. Nyiru camp and kept as a pet. At the time the bird was acquired, it had its full complement of remiges, but no tail had developed.

## FAMILY CAPITONIDAE

*Lybius lacrymosus lacrymosus* (Cabanis)

The spotted-flanked barbet, a common bird of much of Kenya and adjacent areas, was met with on the west base of Mt. Nyiru, on June 22 and 23, when 6 adults, 3 of each sex, were collected. We follow White (1965: 259) in considering the genus *Tricholaema,* formerly used for these birds, as part of *Lybius.*

*Lybius leucomelas diadematus* (Heuglin)

The red-fronted barbet was met with and collected at two localities: plains area 15 miles south of Maralal, June 4, one female with slight gonadal enlargement; west base of Mt. Nyiru, June 24 and 26, two females, one with some ovarian enlargement, the other not.

*Pogoniulus leucomystax* (Sharpe)

This little tinker-bird ranges from central Kenya south to south-central Tanzania. One female, in non-breeding state, was obtained in the Karissia Hills on June 6. It agrees with several from Tanzania in size and coloration. The Karissia Hills must be near the northern limit of the range of this bird.

*Pogoniulus pusillus affinis* (Reichenow)

The red-fronted tinker-bird is represented in the present collection by 1 male and 5 females, all taken in the Karissia Hills, June 2, 3 and 4. The

locality is an additional, but not a surprising, "station" for this tiny barbet, which has an extensive range in the dry bush and acacia country of Kenya. These small barbets fed extensively on a red-berried mistletoe in the Karissia Hills area.

*Pogoniulus bilineatus jacksoni* (Sharpe)

This race of the golden-rumped tinker-bird occurs in the highlands of Kenya, chiefly west of the Rift Valley. Two adult specimens, one of each sex, were collected in the Karissia Hills on June 15. These examples agree with *jacksoni,* not with *alius,* the form found in the areas east of the Rift Valley in Kenya, although the difference between the two is slight.

*Trachyphonus darnaudii bohmi* Fischer and Reichenow

This race of Darnaud's barbet, characterized by having the crown plain black with no terminal orange or red spots on the feathers, ranges farther to the west in northern Kenya than the statements of either Mackworth-Praed and Grant (1957: 735-736) or White (1965: 273) indicate. The present series of 4 specimens from the west base of Mt. Nyiru, June 25 and 26, are clearly *bohmi* and not typical *darnaudii.* The birds collected were in non-breeding condition, and are in somewhat abraded plumage.

*Trachyphonus erythrocephalus versicolor* Hartlaub

This subspecies of the red and yellow barbet, characterized by the yellow forehead and superciliary stripes, is represented in the collection by one adult male, taken on the west base of Mt. Nyiru on June 23. It was in non-breeding condition and is in a molting stage, especially noticeable on the chin and throat.

## FAMILY INDICATORIDAE

*Indicator variegatus Lesson*

The scaly-throated honey-guide is treated binomially to conform with White's list (1965: 274). It is represented in the present collection by one adult male taken in the Karissia Hills on June 3. The bird had the testes considerably enlarged, and is in fairly worn plumage. White is correct in saying that the dimensional characters by which *jubaensis* is characterized form a cline, but this in itself is not impossible of subdivision as the smaller form is, as far as known, a coastal and subcoastal population. Further studies may yet reestablish the usefulness of this racial recognition.

*Indicator indicator* (Sparrman)

The greater honey-guide was met with in the Karissia Hills, June 3, when a non-breeding female adult in good plumage was collected. The species is widely distributed over most of sub-Saharan Africa. Greater honey-guides

were noted as common in the Mt. Nyiru area and although no specimens were saved as skins, two specimens were liquid preserved for anatomical studies.

*Indicator minor minor* Stephens

The lesser honey-guide is widely distributed over much of Africa. One adult, non-breeding female was collected at the west base of Mt. Nyiru on June 22. The specimen is without a head, as that part was preserved in spirits for anatomical study of the olfactory tract.

## FAMILY PICIDAE

*Campethera nubica nubica* (Boddaert)

The Nubian woodpecker, a common bird in most parts of Kenya, was collected on the west base of Mt. Nyiru, on June 24; one adult male, with enlarged testes, and two adult females with slight gonadal development.

*Dendropicos fuscescens hemprichii* (Ehrenberg)

Two specimens of the cardinal woodpecker are referred to the subspecies *hemprichii*. They are a non-breeding adult female taken 15 miles south of Maralal on June 4, and an adult male (by plumage, although marked female on the label) collected on the west base of Mt. Nyiru, June 26. The reason for calling them *hemprichii* and not *lepidus* is because they have the mantle very distinctly barred, and have little (male) or no (female) greenish or yellowish on the mantle and the underparts. Judging by the maps of the ranges of these two races in Mackworth-Praed and Grant: 1957: 762, 763) Mt. Nyiru must be about where the two come together. In their dimensions (wing 80 in the male, 84 mm. in the female), they are large for *hemprichii* and less than the average for *lepidus*.

*Dendrocopos obsoletus ingens* (Hartert)

The little brown-backed woodpecker is represented by one adult female taken in the Karissia Hills, on June 2. It is in very worn plumage but has some new feathers coming in on the upperparts. This is one of the less frequently observed and collected of the east African woodpeckers, although it is widely distributed in the acacia and bush country. Karissia Hills is a new locality for it.

*Thripias namaquus schoensis* (Rüppell)

This race of the bearded woodpecker, characterized by having the black marking of the auriculars extending postero-ventrally so that it separates the white malar stripes from the white post-ocular area, ranges from Ethiopia to northern Kenya and west to the Ubangi–Shari area. Two specimens were obtained, as follows: Karissia Hills, June 3, one male adult; west base of Mt. Nyiru, June 24, one male. Both of these constitute additional, but not surprising locality records.

### FAMILY ALAUDIDAE

*Mirafra africanoides intercedens* Reichenow

One specimen of this widely distributed lark was obtained in the Karissia Hills on June 12, a male with fairly large testes. The bird is darker, deeper chestnut on the auriculars, top of head, and the upperparts generally, and with more extensive blackish fuscous centers on the dorsal feathers, than in most of the comparative material examined, but is approached fairly closely by another male from Kajiado, Rift Valley, Kenya. The Karissia Hills bird is lacking some of its tail feathers, probably as a result of the shot as it shows no sign of molting.

*Eremopteryx leucopareia* (Fischer and Reichenow)

Fischer's sparrow-lark ranges from northern Kenya south across Tanzania, in fairly dry open country. One female, ovary slightly enlarged, was collected in the Karissia Hills, on June 10.

### FAMILY MOTACILLIDAE

*Motacilla alba vidua* Sundevall

One example of the African pied wagtail, an adult male with fairly large testes, was collected in the Karissia Hills, on June 19. This is a common, wide-ranging bird over much of Kenya.

*Anthus leucophrys* subsp.

One male example of this pipit was obtained in the Karissia Hills, on June 12. The single specimen obtained is immature and is not fully grown. It is, therefore, not identifiable to subspecies. According to Hall (1961: 262), the races *zenkeri* and *goodsoni* intergrade just west of the Karissia Hills. It is possible that the present specimen should be considered as *goodsoni,* but to label it so would give it a definiteness that might prove misleading. We are indebted to M. A. Traylor of the Field Museum of Natural History for his opinion on our bird and for comparing it with material in the van Someren collections under his care.

### FAMILY TIMALIIDAE

*Turdoides plebejus cinereus* (Heuglin)

Four specimens of the brown babbler were taken in the Karissia Hills on June 12, one adult male with fairly large testes, one female in breeding condition, and two young females.

*Argya rubiginosa rubiginosa* (Rüppell)

The rufous chatterer is represented in the collection by two males, in non-breeding state, taken on the west base of Mt. Nyiru on June 24.

### FAMILY PYCNONOTIDAE

*Pycnonotus barbatus tricolor* (Hartlaub)

The common, ubiquitous yellow-vented bulbul was collected in the Karissia Hills, on June 3 and 4, three adult males and two adult females, all in non-breeding condition. In calling these birds *tricolor,* and not *fayi,* we are following White (1962: 74), who considers the latter name a synonym of the former. The Samburu district is in the area where *tricolor* and *dodsoni* intergrade.

*Phyllastrephus fischeri placidus* (Shelley)

This race of Fischer's greenbull inhabits highland forests from Marsabit south across central Kenya and Tanzania to northern Mozambique. It was found to be common in the Karissia Hills, where a series of six adults, three of each sex, were collected June 8 to 14. The birds showed some to very great gonadal enlargement.

*Nicator chloris gularis* Hartlaub and Finsch

The east African race of the nicator was met with in the Karissia Hills, where an adult male with greatly enlarged gonads was collected on June 6. The specimen shows signs of active molting in the tail; the plumage of the anterior underparts is much abraded.

### FAMILY MUSCICAPIDAE

*Muscicapa adusta interposita* (van Someren)

Three examples of this race of the pygmy flycatcher were obtained in the Karissia Hills, June 18 and 20, one non-breeding adult of each sex and one young bird.

*Melaenornis chocolatina fischeri* (Reichenow)

The white-eyed slaty flycatcher, here treated as a race of *Melaenornis chocolatinus* to conform with the arrangement of White (1963: 15), was common in the Karissia Hills, where one adult male with somewhat swollen testes, one female with slightly enlarged ovary, and three non-breeding females were collected June 2 to 12. The male is in very worn plumage; the females vary somewhat in the degree of feather abrasion, but are in better plumage than the male.

*Melaenornis pammelaina* (Stanley)

The shining black flycatcher is represented in the collection by six specimens from two localities, as follows: west base Mt. Nyiru, June 24 to 26, one non-breeding adult male and two adult females; Karissia Hills, June 8 and 12, one adult male and one adult female both with somewhat swollen gonads, and one immature female still in the spotted plumage.

*Bradornis microrhynchus* Reichenow

One of these small grayish flycatchers was obtained on the west base of Mt. Nyiru, on June 26. It was sexed as a female, but with a query. It is in fairly fresh plumage.

*Bradornis pallidus subalaris* Sharpe

The pale flycatcher was met with on June 16 when one adult female and one unsexed young bird were collected 5 miles south of Maralal. The female was laying, and had a large ovum in it.

*Batis molitor* (Hahn and Kuster)

The Kenya chin-spot flycatcher was collected in three localities, as follows: Karissia Hills, June 3 and 7, one of each sex with slightly enlarged gonads; 5 miles west of Maralal, June 16, one adult male, two adult females, all in non-breeding state; west base of Mt. Nyiru, June 26, one adult male with slightly swollen testes.

*Terpsiphone viridis ferreti* (Guerin)

This paradise flycatcher was obtained in two localities: on the west base of Mt. Nyiru, June 22, one non-breeding female; Karissia Hills, June 8 and 11, three non-breeding females.

## FAMILY TURDIDAE

*Cercotrichas leucophrys leucoptera* (Rüppell)

The white-browed scrub robin was met with on the west base of Mt. Nyiru where two males were collected on June 24 and 26. One had small gonads, the other showed some testicular swelling. White (1962) has combined *Erythropygia* with *Cercotrichas,* and we place the present species under the latter generic name to conform to his list.

*Cichladusa guttata rufipennis* Sharpe

The single specimen of the spotted morning warbler, obtained on the west base of Mt. Nyiru, June 22, agrees in coloration and in size with two from the lower Tana Valley, and is therefore placed with the race *rufipennis.* No examples of typical *guttata* have been available for comparison. Mt. Nyiru must be close to the meeting ground of the two races. The present example shows signs of molt, especially in the tail; it had the ovary slightly enlarged.

*Myrmecocichla aethiops cryptoleuca* Sharpe

The Kenya anteater-chat was collected in the Karissia Hills; one adult male with somewhat enlarged testes, June 19.

*Monticola rufocinerea rufocinerea* (Rüppell)

The lesser rock thrush was met with on Mt. Nyiru, when an immature

male was collected on June 23 and an adult of the same sex on June 27. We here follow White (1962: 120) in considering *tenuis* the same as typical *rufocinerea,* and find the present birds agree in tone of coloration with others from Mt. Moroto.

*Cossypha heuglini heuglini* Hartlaub

The white-browed robin chat is widely distributed over much of Eastern Africa. Six adults were obtained in the Karissia Hills, June 4 to 8, four males and two females; the birds vary in their gonadal development from not at all enlarged to fairly much so. In the case of one of the males, the testes were noted as black. In addition to these adults, one immature female was collected, in the same place, on June 4.

*Cossypha caffra iolaema* Reichenow

The Kenya robin-chat ranges from northern Mozambique to the highlands of Kenya and northwest to the mountains of southern Sudan. One young, unsexed specimen was taken on the west base of Mt. Nyiru on June 21.

*Turdus abyssinicus abyssinicus* Gmelin

This thrush is represented by one immature female and one adult male, taken on the crest of the Karissia Hills on June 20. The latter bird had enlarged gonads, and is in abraded plumage, possibly a bird that was about through with breeding for the season.

*Turdus pelios centralis* Reichenow

Two specimens of the Kurrichane thrush were obtained in the Karissia Hills, an immature female on June 6, and an adult, non-breeding female on June 12.

FAMILY SYLVIIDAE

*Apalis cinerea cinerea* (Sharpe)

Two adult males of the grey apalis were obtained in the Karissia Hills on June 20; one had the testes small, the other somewhat enlarged; both are in fairly worn plumage.

*Apalis flavida malensis* Neumann

This race of the poorly named black-breasted apalis is represented by one adult of each sex, taken in the Karissia Hills, June 6 and 7.

*Apalis porphyrolaema* Reichenow and Neumann

Two adults, one of each sex, of the chestnut-throated apalis were collected in the Karissia Hills, on June 20. Both showed only slight gonadal enlargement; the male is in molt, especially in the tail. These two birds, together with a male from South Kinangop Plateau, Aberdare Mountains, are very slightly

grayer, less tinged with brownish, above than others from Kaptagat Forest, Eldoret District, from Ol Kalow, and from Naro Maru, Mt. Kenya.

*Apalis rufifrons smithii* (Sharpe)

The red-faced apalis was met with in the plains area at the south end of Mt. Nyiru, where one adult male was taken on June 23. It showed slight gonadal enlargement, and is in somewhat worn plumage.

*Sylvietta whytii jacksoni* Sharpe

Two adults, one male, one female, of this race of the red-faced crombec were collected on the west base of Mt. Nyiru on June 22. Both specimens are somewhat abraded and were in non-breeding condition.

*Cisticola chiniana humilis* Madarasz

The Kenya highlands race of the rattling cisticola was met with in the Karissia Hills where an adult female was taken on June 2 and a male on June 8. The female had the gonads slightly enlarged, the male more so.

*Camaroptera brachyura griseigula* Sharpe

The Taita gray-backed camaroptera was very common in the Karissia Hills, where a series of seven males and three females was collected June 2 to 25. One of the females is a young bird and has the entire upperparts tinged with greenish, and the breast and upper abdomen obscurely streaked or clouded with greenish gray. The adults varied in the state of their gonads from not at all enlarged to fairly large.

*Camaroptera simplex simplex* (Cabanis)

Three adult male gray wren warblers were collected on the west base of Mt. Nyiru, June 22, 25 and 26, all in somewhat abraded plumage, and all with the testes somewhat enlarged.

*Eremomela icteropygialis griseoflava* Heuglin

One unsexed but adult yellow-bellied eremomela was collected in the plains area 15 miles south of Maralal on June 7. It agrees with the characters of *griseoflava,* but also suggests those of *abdominalis,* which race White (1962: 721) records from as far north as Archer's Post and Meru. It seems that the range given for *abdominalis* in Mackworth-Praed and Grant (1955: 432) should be extended northward a very considerable distance. Our present bird agrees with *abdominalis* in lacking the white supraorbital streak, and disagrees with the description of *griseoflava* in Mackworth-Praed and Grant, who write that from the chin to the upper abdomen the plumage is white or buffish white. Our present specimen has these parts pale purplish slate gray, and this appears to be the normal thing, not white as in their description.

### FAMILY HIRUNDINIDAE

*Psalidoprocne pristoptera massaica* Neumann

The black rough-winged swallow was met with in the Karissia Hills, June 3 to 15, when a series of 7 specimens, 3 males, 2 females, 2 unsexed, was collected. Three of these birds are molting in the wings and tail. In two the long rectrices are only partly grown, causing them to appear short-tailed, the depth of the fork being 12 and 15 mm., respectively, as opposed to 35 to 45 mm. in the others. These two birds are also slightly brownish, less deep black than the others, and may be immature birds.

### FAMILY CAMPEPHAGIDAE

*Coracina caesia pura* (Sharpe)

The gray cuckoo-shrike is a bird of the wooded highlands. Three male specimens were collected in the Karissia Hills on June 14; all had somewhat enlarged testes, black in color.

*Campephaga quiscalina martini* Jackson

One adult female of the purple-throated cuckoo-shrike was obtained in the Karissia Hills on June 19, a bird in non-breeding condition.

*Campephaga phoenicea flava* Vieillot

The black cuckoo-shrike was collected in two localities, as follows: Karissia Hills, June 14 and 18, one adult male with enlarged testes, and one immature female; Mt. Nyiru, June 22 and 26, two adult females with small ovaries.

### FAMILY DICRURIDAE

*Dicrurus adsimilis divaricatus* (Lichtenstein)

This drongo is one of the common birds of the east African bush country. One adult female, in non-breeding condition, was collected in the Karissia Hills on June 12. It is in molt in the wings (outer remiges), it appears to be fully adult but has narrow white tips on the under tail coverts, recalling the immature plumage to that extent, but not elsewhere.

### FAMILY LANIIDAE

*Nilaus afer minor* Sharpe

The Somali brubru was met with on Mt. Nyiru, where two adults, one of each sex, were collected on June 24 and 26; both birds were in non-breeding condition.

*Dryoscopus gambensis malzacii* (Heuglin)

This puff-back, characterized by its grayish scapulars and relatively heavy mandible (as compared with *D. cubla*), is represented in the collection by

one adult male with somewhat swollen testes and one non-breeding adult female, both taken in the Karissia Hills, June 6 and 14. The female may have been wrongly sexed as it is just as dark blue black above as the male, not earth-brown as described by Mackworth-Praed and Grant (1955: 620).

*Tchagra jamesi jamesi* (Shelley)

The three-streaked tchagra occurs in northern Kenya north to Ethiopia and Somalia. One adult female, in non-breeding state, was collected on the west base of Mt. Nyiru, June 24.

*Tchagra australis emini* (Reichenow)

This race of the brown-headed bush-shrike, somewhat darker brown above than *T. a. minor* (specimens seen from Nawisha and Kapenguria), was collected in the Karissia Hills, June 3 and 6, where one breeding female and one non-breeding male were taken. The Karissia Hills must be close to the northeastern edge of the range of the race. White (1962: 21) does not even include Kenya in its range, although listing Uganda; Mackworth-Praed and Grant (1955: 626) do record it from western Kenya.

*Tchagra cruenta hilgerti* (Neumann)

The Somali rosy-patched shrike was fairly numerous at the west base of Mt. Nyiru, where two adults of each sex were collected June 23, 24 and 25. All the birds had the small, resting gonads of the non-breeding season.

*Laniarius ferrugineus ambiguus* Madarasz

The boubou shrike was very common in the Karissia Hills, where six adults, three of each sex, were obtained June 2 and 3. One of the males and one of the females were in full breeding condition; the others were not.

*Laniarius funebris* (Hartlaub)

The slate-colored boubou shrike was common on Mt. Nyiru, June 21-26, when seven examples were collected; one immature female molting into adult plumage, three adult females, one adult male, and two unsexed adults. One of the females had the ovary enlarged, the others and the male had small gonads.

*Malaconotus sulfureopectus similis* Smith

Two examples of the sulphur-breasted bush-shrike, one of each sex, were taken in the Karissia Hills, June 4 and 6. This is a widely distributed species in Kenya.

*Lanius dorsalis* Cabanis

One specimen of the Teita fiscal was obtained in the plains area 15 miles south of Maralal, on June 7; an adult male with slightly enlarged testes. The bird is in worn plumage but is molting, especially in the tail. This shrike is

widely distributed in Kenya but tends to be local and hence very uneven in its local status.

*Lanius collaris humeralis* Stanley

The long-tailed fiscal is represented in the collection by one adult male taken in the Karissia Hills, June 15. The bird had the testes slightly enlarged.

### FAMILY PARIDAE

*Parus albiventris* Shelley

The white-breasted tit occurs in forested areas, scrub, and bush country. Three examples were obtained, as follows: Karissia Hills, June 6, one adult male with enlarged testes; 5 miles west of Maralal, June 16, one adult of each sex with slightly enlarged gonads.

### FAMILY CORVIDAE

*Corvus rhipidurus* Hartert

One adult male of the fan-tailed raven was collected 25 miles south of Baragoi, June 21, a bird in non-breeding condition.

*Corvus albicollis* Latham

The white-necked raven is represented in the collection by one adult female, non-breeding state, taken on the west base of Mt. Nyiru on June 22. The bird has an abnormal bill, apparently due to a mishap sometime prior to its death, giving it almost a small, narrow casque on the base of the culmen.

### FAMILY ORIOLIDAE

*Oriolus larvatus rolleti* Salvadori

The black-headed oriole was common in the woodlands of the Karissia Hills where a series of six specimens was collected, June 2 to 18; three adult males with enlarged gonads, one adult female with somewhat swollen ovary, and one immature bird of each sex. The last two have the breast streaked with black, the chin and throat streaked black and yellow. The adults have red bills, the immature ones black. One of the adults shows sign of molt in the wings. Several occupied nests were noted in the large fever trees at the Karissia Hills camp.

### FAMILY STURNIDAE

*Lamprotornis chalybeus cyaniventris* (Blyth)

The blue-eared glossy starling is a common bird in much of Kenya. Five specimens were collected, as follows: plains area 15 miles south of Maralal, one adult female in non-breeding state, two immature females, June 4; west base of Mt. Nyiru, one immature male, June 24, and one adult female, June 27, ovary not enlarged.

*Cinnyricinclus leucogaster verreauxi* (Bocage)

The violet-backed starling is represented in the collection by two males taken in the Karissia Hills, June 11. One is in full adult plumage, the other is molting into the adult feathering.

*Spreo superbus* (Rüppell)

The superb starling was very common in the areas visited by the expedition. In the plains area 15 miles south of Maralal, June 4 to 7, three adult males, one immature male, and two adult females were obtained; in the Karissia Hills one immature male was collected on June 12. In addition, three adult males were collected at the west base of Mt. Nyiru on June 27. One adult female was also obtained with them.

*Creatophora cinerea* (Menschen)

The wattled starling, a well-known bird of much of Africa, was collected as follows: plains area 15 miles south of Maralal, June 7, one adult female with slightly enlarged gonads; June 12, one adult male with swollen testes; Karissia Hills, June 12, one adult male with large testes. The wattles are well developed in the Maralal male, not in the other.

*Buphagus erythrorhynchus* (Stanley)

The red-billed ox-pecker is represented in the collection by four examples, as follows: Karissia Hills, June 12, one adult female; west base of Mt. Nyiru, June 24, one adult male with somewhat enlarged gonads; also two adult males were taken on the west base of Mt. Nyiru June 27, one with small and the other with enlarged testes.

## FAMILY NECTARINIIDAE

*Anthreptes collaris garguensis* Mearns

This race of the collared sunbird is represented by two adult males and one adult female, taken in the Karissia Hills, June 7 to 19. None of the birds was in breeding condition.

*Nectarinia amethystina kirkii* (Shelley)

One adult of each sex of the amethyst sunbird was collected in the Karissia Hills, June 11 and 18.

*Nectarinia venusta falkensteini* (Fischer and Reichenow)

The Kenya buff-breasted sunbird was taken at two places, as follows: Karissia Hills, June 12 and 18, one adult of each sex; west base of Mt. Nyiru, June 26, one adult male; all in non-breeding state.

*Nectarinia preussi kikuyuensis* Mearns

This race of the double-collared sunbird is represented by three speci-

mens, two adult males and one adult female, all taken in the Karissia Hills, June 15 to 20.

*Nectarinia mariquensis osiris* Finsch

The mariqua sunbird was extremely common on the west base of Mt. Nyiru, June 22 to 25, where a series of five adult males, one immature male, and three adult females was collected. The immature male is molting into adult plumage. Two of the females have the chin and middle of the throat solid blackish; the other has these areas, as well as the upper and lateral parts of the abdomen, streaked with blackish.

## FAMILY ZOSTEROPIDAE

*Zosterops senegalensis jacksoni* Neumann

Jackson's white-eye was very numerous in the Karissia Hills, where a series of seven adult females was obtained June 6 to 14. The absence of males in this series is puzzling as usually the sexes are found together in the same loose flocks during the non-breeding season. All the hens collected had small gonads, and were non-breeding birds.

## FAMILY PLOCEIDAE

*Ploceus baglafecht reichenowi* (Fischer)

One example of this wide-ranging weaver was obtained in the Karissia Hills, June 8, an adult male with somewhat enlarged testes.

*Ploceus velatus uluensis* (Neumann)

The masked weaver was met with on the west base of Mt. Nyiru, where one male, almost, but not quite, in adult plumage, was collected on June 27.

*Ploceus melanogaster stephanophorus* (Sharpe)

One adult female of this black-billed weaver was collected in the Karissia Hills, on June 14; it had the ovary slightly enlarged.

*Malimbus rubriceps leuconotus* (Muller)

The red-headed weaver was collected in two places, as follows: Karissia Hills, June 12, one adult male with somewhat swollen gonads; west base of Mt. Nyiru, June 22, one immature male.

*Dinemellia dinemellii dinemellii* (Rüppell)

This noisy, conspicuous weaver was met with 25 miles south of Baragoi, where two adult females were collected on June 21.

*Plocepasser mahali melanorhynchus* Bonaparte

The black-billed sparrow-weaver was common on the west base of Mt.

Nyiru, where four adult females and one immature female were collected on June 22 and 24. The specimen marked as immature is similar to the adults.

*Pseudonigrita arnaudi arnaudi* (Bonaparte)

The gray-headed social weaver is represented in the collection by three examples, as follows: plains area 15 miles south of Maralal, June 7, one adult, non-breeding female; June 17, one adult male with somewhat enlarged testes; Karissia Hills, June 11, one adult male with somewhat swollen gonads.

*Passer iagoensis rufocinctus* Finsch and Richenow

Two examples of the Kenya rufous sparrow were collected in the plains area 15 miles south of Maralal, a female on June 4, and a male on June 7; both birds showed slight gonadal enlargement. The male is in very abraded plumage.

*Petronia xanthocollis pyrgita* (Heuglin)

The yellow-spotted petronia is represented in the collection by one adult, non-breeding male, taken in the Karissia Hills on June 12.

*Estrilda paludicola paludicola* Heuglin

This rather local waxbill was found in the Karissia Hills on June 20 when two non-breeding females were collected. In Kenya this species is found only in the more western half of the country; the Karissia Hills may be close to the eastern limit of its range.

*Estrilda ianthinogaster* (Reichenow)

The Kenya grenadier was common on the west base of Mt. Nyiru, where four examples were taken June 22 and 24; two adult males in non-breeding state, one immature male, and one non-breeding adult female.

*Estrilda bengala bengala* (Linnaeus)

The red-cheeked cordon-bleu is represented in the collection by two adults, both with large gonads, taken in the Karissia Hills, June 8. The female had a large developing egg.

## FAMILY EMBERIZIDAE

*Emberiza flaviventris kalaharica* Roberts

One adult male, taken in the Karissia Hills on June 4, represents this bunting. It is in fairly worn plumage.

*Emberiza tahapisi tahapisi* Smith

The cinnamon-breasted rock bunting was met with on the west base of Mt. Nyiru on June 25 when an adult male with slightly swollen gonads was collected.

### FAMILY FRINGILLIDAE

*Serinus sulphuratus sharpii* Neumann

One adult female brimstone canary was collected 5 miles west of Maralal on June 16. It had a slightly enlarged ovary.

*Serinus striolatus striolatus* (Rüppell)

The streaky seed-eater is represented in the collection by one adult, non-breeding female, taken in the Karissia Hills, June 20.

*Serinus reichardi striatipectus* (Sharpe)

Three adult females of this seed-eater were obtained on the west base of Mt. Nyiru, June 25; one had the ovary enlarged, the other two did not.

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UMBER 131 FEBRUARY 20, 1968

## ON THE AGE DISTRIBUTION OF *SMILODON CALIFORNICUS* BOVARD FROM RANCHO LA BREA

*By* GEORGE J. MILLER

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DOROTHY M. HALMOS
*Editor*

# ON THE AGE DISTRIBUTION OF *SMILODON CALIFORNICUS* BOVARD FROM RANCHO LA BREA

*By* George J. Miller[1]

Abstract: Skulls of over 2100 specimens of *Smilodon californicus* Bovard from the collection of the Los Angeles County Museum of Natural History are studied in an effort to determine the percentages of the various age groups that were trapped in the La Brea Pits. The specimens are arbitrarily classified as Juvenile, Young Adult, Adult, and Aged, using tooth wear and closure of the basioccipital-basisphenoid suture as criteria. The percentages of the four age groups are found to be as follows: 16.6% Juveniles, 23.2% Young Adults, 17.2% Adults, and 8.5% Aged, with 34.5% undetermined. The large number of undetermined, consisting mostly of adults that could not be positively classified as Young Adults, Adults, or Aged, are then classified with the Aged category eliminated, giving the following breakdown: 16.6% Juveniles, 25.7% Young Adults, 56.5% Adults, and 1.2% undetermined. These data show that a cross section of the *Smilodon californicus* population, rather than a preponderance of any one age group, was trapped in the tar pits.

## Introduction

For the past 45 years the Rancho La Brea Fauna has been recognized by paleontologists as the outstanding collection of Pleistocene life available for study (Stock, 1961). Of the many large mammals trapped and preserved in the tar pools, those found in the greatest abundance are *Canis dirus* (the dire wolf), with from 1646 (Marcus, 1960) to 2000 specimens (Stock, 1929a); and *Smilodon californicus* Bovard, (the sabre-tooth cat), with from 1029 (Marcus, 1960) to 1500 specimens (Stock, 1929a). The excellent state of preservation of this material (Stock, 1929b and 1961), together with its abundance, suggests many possibilities for population, variation, extinction, and microevolution studies. In the hope that the information obtained will be of value in the furtherance of the studies mentioned above, the present study attempts to determine the age distribution of *Smilodon californicus* from an examination of the skulls of the animals that were trapped in the tar pits. The term "skull," as used in this paper, denotes any cranial specimen of sufficient completeness to determine the age. *S. californicus* was chosen for this study over *Canis dirus* for convenience only—the *Smilodon* material is more readily accessible. It is hoped that a similar study will be done in the near future on *C. dirus*.

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## MATERIAL STUDIED

Skulls and parts of skulls of *Smilodon californicus* from the collection of the Los Angeles County Museum of Natural History were used exclusively in this study. All available catalogued and uncatalogued specimens were examined and taken into consideration (fifty of the 576 catalogued skulls were out on loan and therefore unavailable for study). Out of over 2100 specimens examined, 918 were, for reasons discussed below, found to be suitable for this study.

## PROCEDURE

Lack of knowledge of the life span and the rate of maturation of *Smilodon* made it impossible to determine exact age groups, so arbitrary age groups were used (it was not deemed advisable to extrapolate from knowledge of recent carnivores because of the different patterns of tooth wear brought about by *Smilodon's* unique dentition). The age groups were designated as Juvenile, Young Adult, Adult, and Aged.

The Juvenile group includes all skulls with any deciduous dentition or alveoli for deciduous dentition and with no wear on any of the permanent dentition (Figures 1 and 2). This group is probably under-represented because of separation and fragmentation of the soft-boned young skulls with their incompletely sealed sutures (churning, or movement of the petroliferous mass in the tar pits, had a tendency to cause breakage and separation of bones and skeletons as well as cause the phenomenon known as pit wear). Complete skulls of Juveniles are rare (out of 150 Juvenile specimens examined, there were nine complete skulls, and the preparator had wired these together at the sutures as shown in Figure 3); most of the specimens in this age group consist of fragments (Fig. 4). Many skulls and fragments of skulls in this and in other age groups were not used in this study because of the possibility of duplication. When the uncatalogued fragmentary specimens were examined, all pit data were checked, and when a left and right part of an animal of the same age with the same pit data was found only one part of the animal was listed. Although this procedure could cause the elimination of some specimens from the study, any possibility of counting the same animal twice is avoided. As the workers who originally catalogued the fossils from Rancho La Brea are believed to have been extremely accurate (Leslie F. Marcus, 1966, personal communication), this study has not questioned possible duplication of any of the catalogued material.

Skulls with all permanent dentition or alveoli for permanent dentition and no deciduous dentition or alveoli were classified as Young Adults. Other criteria used for this group were: no wear on the incisors, canines, or P3; less than one millimeter of wear on the paracone of the P4 (Figures 5 and 6); and the open basioccipital-basisphenoid suture (Fig. 7). It was observed during the course of this investigation that closure of the basioccipital-

*Figure 1.* (Upper) *Smilodon californicus* Juvenile. Lingual view of deciduous right C and M3 and right permanent C and P4. Permanent dentition not completely erupted (LACM 2001-30).

*Figure 2.* (Lower) *Smilodon californicus* Juvenile. Lingual view of deciduous right M3 and permanent right P4. Permanent dentition not completely erupted and showing no wear (LACM 2001-104).

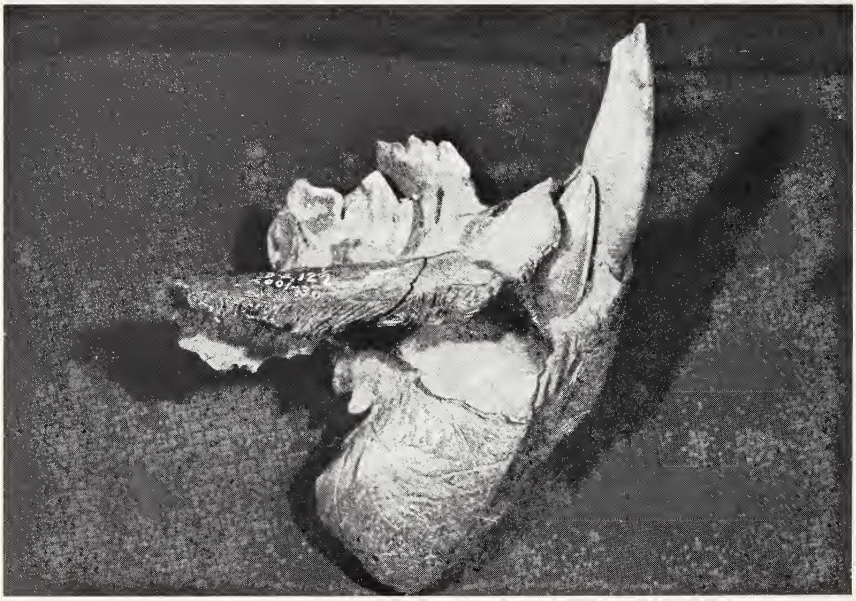

*Figure 3* (Upper) *Smilodon californicus* Juvenile. Ventral view of one of the few complete Juvenile skulls recovered from the La Brea Pits (LACM 2001-104).

*Figure 4.* (Lower) *Smilodon californicus* Juvenile. Typical skull fragment showing upper right permanent and deciduous dentition (LACM 2001-30).

basisphenoid suture coincided with the completion of the emergence of the permanent dentition; therefore, this feature was also used to classify the Young Adults.

Presence of all permanent dentition or alveoli; moderate wear on the canines, incisors, and P3; the paracone and metacone of the P4 worn from one millimeter to one centimeter from the alveolar border (Fig. 8); and the closed basioccipital-basisphenoid suture (Fig. 9) were used as criteria for the Adult grouping.

Extreme wear on all dentition and the P4 worn from one centimeter above the alveolar border to the alveolar border (Fig. 10) were the characteristics used to classify the Aged. Some carnassials were found that were worn through to the pulp cavity as shown in Figure 11. A tooth worn to this extent would not be likely to last much longer so animals with this condition were considered to be near the end of their life span and were therefore classified as Aged.

When a division was made between the Adults and Aged groups, the amount of wear on the P4, unless caused by malocclusion, took precedence over other criteria. Extensive wear was sometimes found on one carnassial and not on the other and was thus considered to be caused by malocclusion rather than by age. Although there are two hypotheses to explain the mode of existence of *Smilodon* (some authorities consider *Smilodon* to have been a fierce predator, whereas others consider him to have been a scavenger or carrion feeder), the carnassial would seem to have been essential to the animal in either case. Another possible cause of extensive wear could be additional use of the carnassials brought about by loss of the canines (Stock, 1961).

Use of closure of the basioccipital-basisphenoid suture as a means of age determination was justified, as discussed above, by the fact that closure was observed to coincide with the emergence of the permanent dentition. Furthermore, the location of the suture at a sturdily constructed area of the skull prevented its opening on Aged specimens that had been subjected to pit churning. Aged skulls were found that had undergone severe strain, with many of the other sutures opened, but still having the basioccipital-basisphenoid suture closed.

## RESULTS

Counts taken during this study show that a total of at least 2400 *Smilodon* skulls have been collected from Rancho La Brea, approximately 2100 of these being in the collection of the Los Angeles County Museum of Natural History. This count is somewhat more than that of Stock's (1929) census with 1500 specimens and Marcus' (1960) census with 1029 specimens; however, these censuses were taken using bones other than the skull. The discrepancies may possibly be accounted for by Marcus' (1960)

*Figure 5.* (Upper) *Smilodon californicus* Young Adult. Lingual view of permanent left P3, P4, and M1 showing less than one millimeter of wear on the paracone of the P4 (LACM 2001-101).

*Figure 6* (Lower) *Smilodon californicus.* Young Adult. Lingual view of permanent left P3 and P4 showing one millimeter of wear on the paracone of the P4 (LACM 2001-290).

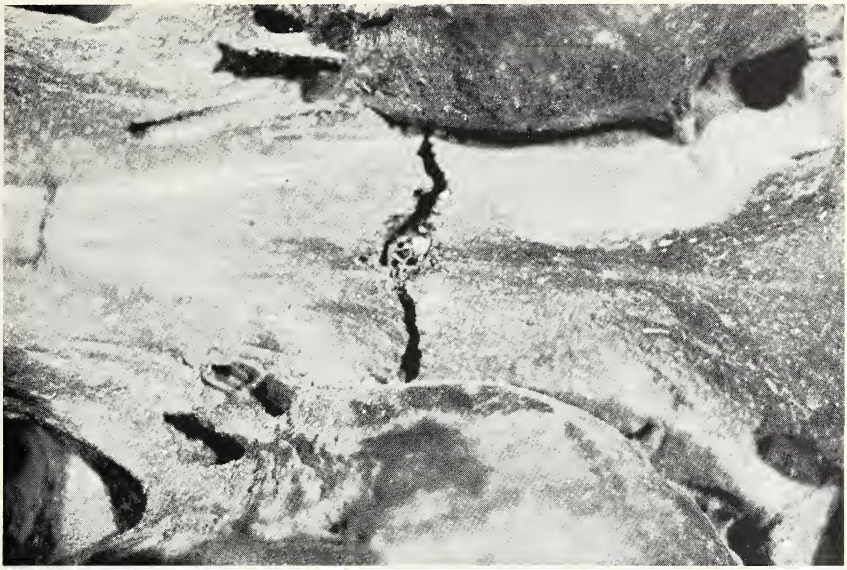

*Figure 7.* (Upper) *Smilodon californicus* Young Adult. Ventral view of skull showing basioccipital-basisphenoid suture not closed (LACM 2001-101).

*Figure 8.* (Lower) *Smilodon californicus* Adult. Lingual view of permanent left P3 and P4 showing more than one millimeter of wear on the paracone and metacone of the P4 (LACM 2001-250).

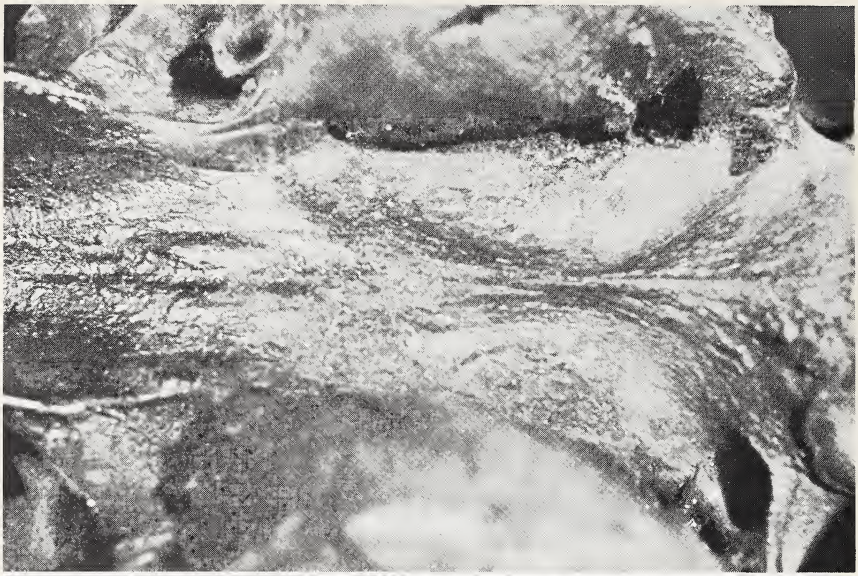

*Figure 9.* (Upper) *Smilodon californicus* Adult. Ventral view of skull showing basi-occipital-basisphenoid suture closed (LACM 2001-96).

*Figure 10.* (Lower) *Smilodon californicus* Aged. Lingual view of permanent left P4 showing tooth worn down to within one centimeter of the alveolar border (LACM 2001-102).

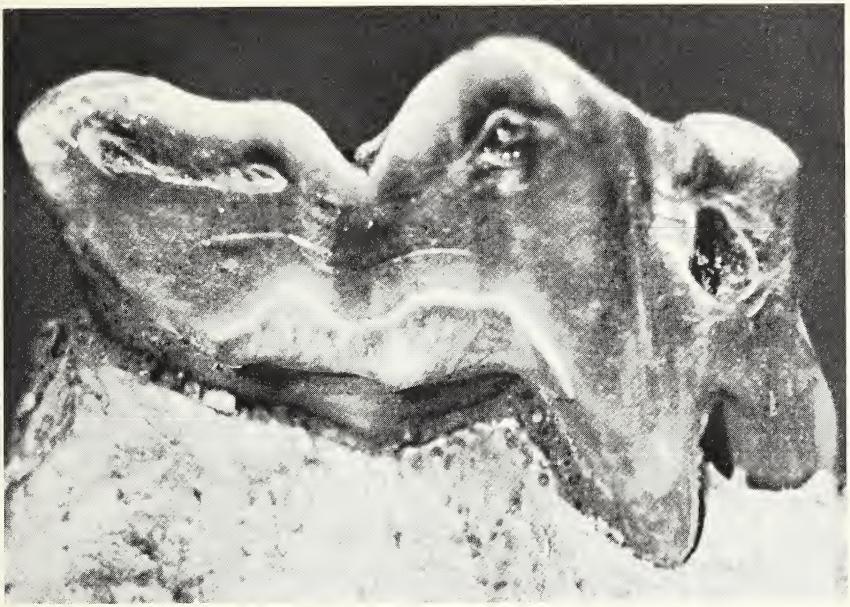

*Figure 11. Smilodon californicus* Aged. Lingual view of permanent right P4 showing tooth worn through to the pulp cavity (LACM 2001-297).

Selection Hypothesis, in which he suggests the possibility of selective preservation and of selective collection. The Rancho La Brea field notes show that during excavation of the pits a great many specimens were discarded as being too poorly preserved to merit retention (Wyman, 1913). Many collectors have a tendency to be more selective when collecting a rich deposit than they would be under more normal circumstances and it seems that the La Brea collectors were affected by this human weakness. There are 576 catalogued skulls in the Los Angeles County Museum of Natural History collection, 50 of which were out on loan and thus not studied; 342 uncatalogued but identifiable; and over 1350 uncatalogued fragmentary specimens which were not suitable for this study, making a total of at least 2100 specimens in the Los Angeles County Museum collection. A recent census of the collection at the University of California at Berkeley (John E. Mawby, 1966 personal communication) showed 111 skulls and fragments of skulls (an additional 62 fragmentary specimens in this collection are probable duplications). Many skulls from the Berkeley collection have been loaned or traded; it is probable that the collection originally contained at least 200 skulls. Data were not available on the smaller collections made by Occidental College, Los Angeles High School, and other institutions. If these

smaller collections are disregarded, there is a total of at least 2100 skulls, 918 or 43.7% of which were suitable for or available for and used in this study. It must be emphasized that the 2100 skulls include many fragments and thus may give an exaggerated picture of the number of animals represented. It is quite probable that many of these fragments are from the same animal. This probable variable, as mentioned above, was taken into account in this investigation.

Table 1 shows a breakdown of the data obtained into four age groups: Juvenile, Young Adult, Adult, and Aged, with an undetermined group consisting of 11 Juveniles, 24 Juvenile or Young Adult fragments, and 283 Adults. Because the 11 Juveniles are possible duplications, they are not included in the classification. The 283 Adults could not be classified as Adults or Aged because of their poor condition—too many teeth missing in some, and difficulty in distinguishing between age and pit wear in others; however, they could all be positively identified as mature adults by closure

TABLE 1
FREQUENCY IN NUMBER AND PERCENT OF INDIVIDUALS OF EACH AGE GROUP

| *Age Group* | *Frequency in Number of Individuals* | *Percent of Individuals* |
|---|---|---|
| Juveniles | 150 | 16.6 |
| Young Adults | 213 | 23.2 |
| Adults | 158 | 17.2 |
| Aged | 79 | 8.5 |
| Undetermined | 318 | 34.5 |
| Totals | 918 | 100.0 |

TABLE 2
FREQUENCY IN NUMBER AND PERCENT OF INDIVIDUALS OF EACH AGE GROUP (THREE AGE GROUPS)

| *Age Group* | *Frequency in Number of Individuals* | *Percent of Individuals* |
|---|---|---|
| Juveniles | 150 | 16.6 |
| Young Adults | 237 | 25.7 |
| Adults | 520 | 56.5 |
| Undetermined | 11 | 1.2 |
| Totals | 918 | 100.0 |

of the basioccipital-basisphenoid suture. Although Table 1 shows a good age distribution, 34.5% of the animals studied remain unclassified. It was therefore decided for purposes of comparison to combine the Adults and the Aged and to include the 283 undetermined Adults under the heading of Adults, and to place the 24 fragmentary young specimens under the Young Adult heading to give the results shown in Table 2. The decision to place the 24 young animals in the Young Adult grouping was made by using either tooth wear or closure of the basioccipital-basisphenoid suture as criteria instead of using both as was done in Table 1.

In Table 3 the distribution of the four age groups is shown for the most heavily populated pits. The percentage distribution of the same data is shown in Table 4. The data from Tables 3 and 4 were combined into three age

TABLE 3
FREQUENCY OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(FOUR AGE GROUPS)

| | PIT NUMBER | | | | | | |
|---|---|---|---|---|---|---|---|
| | 3 | 61-67 | 4 | 77 | 13 | 60 | 2 |
| *Age Group* | | | | | | | |
| Juveniles | 61 | 23 | 24 | 7 | 9 | 4 | 4 |
| Young Adults | 56 | 44 | 19 | 7 | 4 | 0 | 3 |
| Adults | 65 | 62 | 26 | 4 | 1 | 3 | 2 |
| Aged | 27 | 33 | 15 | 1 | 1 | 0 | 1 |
| Undetermined | 136 | 95 | 26 | 44 | 43 | 11 | 6 |
| Totals | 345 | 257 | 110 | 63 | 58 | 18 | 16 |

TABLE 4
PERCENT OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(FOUR AGE GROUPS)

| | PIT NUMBER | | | | | | |
|---|---|---|---|---|---|---|---|
| | 3 | 61-67 | 4 | 77 | 13 | 60 | 2 |
| *Age Group* | | | | | | | |
| Juveniles | 17.6 | 9.0 | 21.8 | 11.1 | 15.5 | 22.2 | 25.0 |
| Young Adults | 16.2 | 17.1 | 17.2 | 11.1 | 6.9 | 0.0 | 18.8 |
| Adults | 18.9 | 24.1 | 23.7 | 6.3 | 1.7 | 16.7 | 12.5 |
| Aged | 7.9 | 12.8 | 13.6 | 1.6 | 1.7 | 0.0 | 6.2 |
| Undetermined | 39.4 | 37.0 | 23.7 | 69.9 | 74.2 | 61.1 | 37.5 |

groups (Juvenile, Young Adult, and Adult) in the same manner as described above (the specimens under the undetermined heading were all classified except for the 11 doubtful Juveniles) to give the distribution of the animals in the seven most heavily populated pits as seen in Tables 5 and 6. A total of 867 specimens was used in the pit breakdown, which made a smaller sampling than was used in the over-all distribution because the smaller pits were not included and because skulls without pit data were necessarily eliminated. The data for Pit 61 and Pit 67 were combined because these two pits were actually "one large pit" (Marcus, 1960).

TABLE 5
FREQUENCY OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(THREE AGE GROUPS)

| | PIT NUMBER | | | | | | |
|---|---|---|---|---|---|---|---|
| | 3 | 61-67 | 4 | 77 | 13 | 60 | 2 |
| *Age Group* | | | | | | | |
| Juveniles | 68 | 27 | 25 | 7 | 9 | 5 | 4 |
| Young Adults | 91 | 69 | 22 | 17 | 12 | 0 | 5 |
| Adults | 177 | 161 | 63 | 39 | 37 | 13 | 5 |
| Undetermined | 9 | 0 | 0 | 0 | 0 | 0 | 2 |
| Totals | 345 | 257 | 110 | 63 | 58 | 18 | 16 |

TABLE 6
PERCENT OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(THREE AGE GROUPS)

| | PIT NUMBER | | | | | | |
|---|---|---|---|---|---|---|---|
| | 3 | 61-67 | 4 | 77 | 13 | 60 | 2 |
| *Age Group* | | | | | | | |
| Juveniles | 19.3 | 10.5 | 22.7 | 11.1 | 15.5 | 27.8 | 25.0 |
| Young Adults | 26.5 | 26.8 | 20.0 | 27.0 | 20.7 | 0.0 | 31.3 |
| Adults | 51.6 | 62.7 | 57.3 | 61.9 | 63.8 | 72.2 | 31.3 |
| Undetermined | 2.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 12.4 |

## DISCUSSIONS AND CONCLUSIONS

It is believed that the use of the two different age distributions (Juvenile, Young Adult, Adult, and Aged as opposed to Juvenile, Young Adult,

and Adult), gives a more thorough view of the data than does a single breakdown. Both breakdowns are considered to be of value in that the four-class grouping gives a more detailed picture of the distribution, whereas the three-class grouping includes a larger sampling. It may be noted that the three-class grouping, "youth, middle life, and old age," was favored by Kurtén (1954).

The most likely place for deviation is in the Juvenile category, wherein poor preservation of young animals would result in a low count. The possibility of increased fecundity (Merriam and Stock, 1932) would, however, have a tendency to partially offset this factor. It has been hypothesized that animals on the verge of extinction, undergoing a population decrease, experience an increase in fecundity as a natural compensatory mechanism. This phenomenon may be compared to a similar condition that may be observed on a smaller scale in living populations today during so-called "good years." In a time of drought or other adverse climatic conditions litter size and populations decrease. When environmental conditions improve and the food supply becomes abundant an increase in fecundity may be observed. Favorable conditions would have a tendency to occur when the population is reduced, as the environment would then be more able to meet the needs of the smaller population. There is also the possibility that younger animals with their greater vigor would be better able to avoid being trapped or to escape after being trapped. However, it would seem that the lack of experience of such animals coupled with their youthful exuberance would tend to lead them into more trouble, thus increasing the probability of their blundering into the tar pools. The net result would thus probably be a mutual cancellation of these two factors.

Two possibilities of discrepancies in the division of the Adult and Aged exist because some animals show excessive tooth wear for their age (Kurtén, 1954); and because of difficulty in distinguishing between pit wear and age. Combining these two groups into the Adult grouping, as was done in Tables 2, 5, and 6, eliminated this problem.

Selective preservation and collection (Marcus, 1960) is a possible variable that could not be controlled at this late date.

The age distribution in Table 1 clearly shows that a cross section of the *Smilodon* population was trapped and preserved in the La Brea Pits, rather than a majority of any one age group. Table 1 also shows that there are a sufficient number of specimens from each age group for population, variation, extinction, and microevolutionary studies (it should be recognized that until dating of this material has been accomplished, the collection represents a population over an indefinite period of time). These data also show that at least 8.5% of the *Smilodon* population reached old age.

The need for age dating of the La Brea collection has long been recognized (Howard 1960, Stock 1961); however, very little has been done.

Although work is now in progress on the dating of animal remains and some information has been obtained, all published material to date has been from analyses of wood samples. A "wood sample" from an unidentified pit was dated as 16,325 + or − 2000 years B. P. (Before Present) (Douglas 1952). Howard (1962) commented on the questionable value of this dating because of the lack of proper data on the specimen and because of the method used. Stock (1961) referred to the La Brea fauna as "late middle Pleistocene" and "late Pleistocene." Howard (1960) reported dating of a tree from Pit 3 as 14,500 B. P. + or − 200 years. As Howard observed, "The dating of the tree from pit 3 undoubtedly could apply as well to the fossil bones of the extinct animals . . . . ." It is also possible that the bones found stratigraphically below the tree roots are even older (Hildegarde Howard, 1967, personal communication). However, this is an isolated case. The fortuitous circumstance of a tree rooted in amongst the bones occurred only in one pit. This was the state of things as of 1962. Recent radio-carbon dating by Berger and Libby (1966) has extended the time range for Rancho La Brea considerably as shown below:

| | | |
|---|---|---|
| Pit 4, | 5 foot depth | 33,700 + or − 1600 years B. P. |
| Pit 9, | 8½ foot depth | 13,300 + or − 160 years B. P. |
| Pit 9, | 16 foot depth | > 40,000 years B. P. |
| Pit 16, | 6½ foot depth | > 40,000 years B. P. |
| Pit 16, | 12 foot depth | > 40,000 years B. P. |
| Pit 77, | no record of depth | 37,000 + or − 2660 years B. P. |

Although this gives a much better perspective of the age of some of the pits, this work was also done on wood samples, and any correlation between the wood and the bones is open to question. Due to pit churning the correlation between bones found in any one pit at the same depth and in the same grid may also be questioned. Berger and Libby (1966) also report a date of 23,300 + or − 510 years B. P. for cypress wood and 32,350 + or − 1400 years B. P. for leaves of California live oak from the University of California at Berkeley collection of Rancho La Brea material. Axelrod (1966) used these data for an analysis of the Rancho La Brea flora in which he was able to show that "at least two widely different communities" were "entombed in the tar pits at different times, and under wholly different climatic conditions." Recent (July, 1966) unpublished dating of *Canis dirus* humeri by Geochron Labs., Inc. showed a specimen from Pit 3 at a depth of 22 to 25 feet to have an age of 9860 + or − 550 C-14 years B. P., and a specimen from Pit 16 at 8 to 12 feet to have an age of 10,710 + or − 320 C-14 years B. P. This dating was, however, on carbonate, as it was found to be impractical to date the collagen because of contamination by petroleum and other organic compounds such as paint. (Paint was used by the original curators to label the bone.) New collagen extraction methods

now being developed promise to overcome this difficulty. There is, therefore, still a need for an extensive dating of bone. As will be suggested below, two of the pits may be considered as representative of the over-all distribution of *Smilodon* from La Brea. Possibly the most valuable procedure would thus be to date all of one element from one of the more prevalent animals such as *Smilodon californicus* or *Canis dirus* for one of the more representative pits. As Berger and Libby (1966) show Pit 4 to be one of the oldest pits and Pit 4 will be suggested below to be one of the representative pits, it might be most useful to do this work on Pit 4, although Pit 3 should also be considered as one of the representative pits.

Although Tables 1 and 2 show a larger proportion of Adults than of Juveniles, if the Juvenile and Young Adults are combined and then compared with the adults, a ratio of approximately 56 adults to 42 young is obtained. Without taking into consideration the poor preservation chances of young animals, this ratio is reasonably close to the age distribution (58 adults to 40 young) found in recent living populations of *Panthera (Felis) leo* (Guggisberg, 1963), the only recent large cat for which age distribution data were available. A chi-square test for deviation on these data based on the methods of Simpson, Roe and Lewontin (1960) showed a P value of .7 or no significant deviation from the expected. It may be argued that any comparison between *Smilodon* and the African lion is not necessarily pertinent but there are no data on populations of any size of large carnivores, either fossil or living, available.

The frequency of skulls from the four age groups (Juvenile, Young Adult, Adult, and Aged) in the most heavily populated pits (Tables 3 and 4) shows Pit 3 and Pit 4 to have an age distribution very close to that of all the pits combined (Table 1). Pit 3 and Pit 4 may thus possibly be representative of the Rancho La Brea *Smilodon* population, so either of these two pits could be utilized in a population study instead of studying the entire collection. Although similar frequencies being found in similar or related populations may not necessarily mean that the populations are identical (Leslie F. Marcus, 1967, personal communication), the fact that the age distributions are so nearly alike would seem to justify taking full advantage of the similarities.

The breakdown of the data into three age groups (Juvenile, Young Adult, and Adult) also shows the age distribution of *Smilodon* from Pit 3 and Pit 4 to be in close agreement with the distribution of the entire *Smilodon* collection (Tables 2, 5, and 6).

The conclusion is therefore made that the Rancho La Brea population of *Smilodon californicus,* as represented by the collection of the Los Angeles County Museum of Natural History, is a valid cross section of a population in time and as such, is excellent material for studies of population, variation, extinction, microevolution, and other related paleontological problems.

## ACKNOWLEDGMENTS

I wish to express my profound gratitude to J. R. Macdonald, Senior Curator of Vertebrate Paleontology at the Los Angeles County Museum of Natural History, who suggested this project, for making available to me for study the *Smilodon* collection and associated catalogs and for many valuable suggestions. My thanks are also extended to Chief Curator of Earth Sciences, Theodore Downs, for the much needed background material used in this study. A difficult task was made easy and pleasant by the cooperation of the many people on the staff of the Los Angeles County Museum of Natural History. I would like to extend my deepest thanks to Leonard Bessom, Donald B. (Joe) Cocke, Charles McLaughlin, and Stephen Wright for their generous help in solving my many problems. I am very grateful to Hildegarde Howard for reading the manuscript and offering many helpful suggestions. My special thanks go to Leslie F. Marcus for consultation and advice, of which I took full advantage. I would also like to thank James Asher of the Genetics Department at California State College at Long Beach for his valuable help with mathematical analyses. I would like to extend my special thanks to Professor John A. White, Curator of Vertebrate Paleontology at Idaho State University, for his many valuable suggestions and for his constant encouragement. None of the above-mentioned should be in any way held responsible for the opinions or conclusions expressed in this paper—I am entirely responsible. The specimens in the Los Angeles County Museum of Natural History collection were photographed by the author. This research was partially supported by National Science Foundation Grant GB 5119.

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# CONTRIBUTIONS IN SCIENCE

UMBER 132 FEBRUARY 20, 1968

# TAXONOMIC NOTES ON SOME MEXICAN CEPHALOTINE ANTS (HYMENOPTERA: FORMICIDAE)

*By* ROY R. SNELLING

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DOROTHY M. HALMOS
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# TAXONOMIC NOTES ON SOME MEXICAN CEPHALOTINE ANTS (HYMENOPTERA: FORMICIDAE)

*By* Roy R. Snelling[1]

Abstract: The previously undescribed male of *Procryptocerus scabriusculus* Emery is characterized and figured. *Cryptocerus insularis* Wheeler, previously known only from the lost holotype, is recharacterized and its relationship to *C. rohweri* Wheeler and *C. wheeleri* Forel is discussed. Soldiers and workers of all three are figured and a key is given for their separation.

## **Procryptocerus scabriusculus** Emery, 1894

Figure 1

In his excellent treatment of the cephalotine ants Kempf (1951) divided the genus *Procryptocerus* into a number of species complexes. In his analyses of these complexes he was able to place some names into synonymy; others were elevated to species level, and in general the systematics of the genus was put on a sound basis. Unfortunately, relationships within a given complex were left unresolved due to a lack of adequate representation of the alate forms. One of Kempf's complexes was composed of the forms previously ascribed to *P. striatus* (F. Smith), a starting total of thirteen "subspecies and varieties," which he reduced to seven species. Of these species, males were known and described for only two, *P. adlerzi* (Mayr) and *P. convergens* (Mayr).

While collecting in the vicinity of Cordoba, Veracruz, Mexico, during July, 1965, I was fortunate enough to secure several complete colonies of *P. scabriusculus* Emery, a member of this complex, in two of which were found alate individuals of both sexes. Since the previously undescribed male of this species exhibits a number of interesting characters which readily permit its separation from those of *P. adlerzi* and *P. convergens,* it seems worthwhile to describe it at this time.

The male differs from that of *P. adlerzi* most obviously in the presence of distinct apical spurs on the middle and hind tibiae, a trait which it shares with *P. convergens.* If I correctly understand Kempf's description of the *P. convergens* male, that of *P. scabriusculus* may be separated by the presence of a distinctly shining, sculptureless area on the frons (sculptured throughout in *P. convergens,* according to Kempf), the shorter hairs on the underside of the head (said to be longer than the antennal scape in *P. convergens*), and the decidedly less truncate subgenital plate.

[1]Entomology Section, Los Angeles County Museum of Natural History, Los Angeles, California.

*Male.* Length of body, 7.2 - 8.5 mm; of forewing, 4.8 - 5.7 mm. Distance from anterior ocellus to apical margin of clypeus 0.8 times interocular distance; greatest ocular diameter 0.5 times maximum head length; maximum diameter of lateral ocelli slightly less than minimum distance between them; antennal scape longer than first two funicular segments combined. Mandibles rugosopunctate, with distinct, essentially longitudinal rugulae. Clypeal disc minutely tessellate, laterally with a few short rugulae; apical margin evenly concave medially. Longitudinal rugulae of face variable, rather coarse and close between eyes and antennal sockets; fine, close and parallel between antennal sockets; elsewhere moderately coarse, spacing variable, but absent from triangular area on frons in front of anterior ocellus; inter-rugal sculpturing consisting of very fine tessellation. Occiput rounded, without distinct corners.

Thoracic dorsum in profile not evenly rounded, the scutellum slightly bulging. Shoulders angulate, but not dentate, pronotal sides divergent caudad; pronotal dorsum free of sculpturing, the sides with a few fine striae below. Mayrian furrows of scutum deeply impressed; median lobe with numerous very fine oblique striae anteriorly and posteriorly, medially free of striae. Mesopleurae largely smooth, with a few fine striae below. Base of epinotum with a short triangular tooth on each posterior corner, the discal area with strong, essentially transverse, rugae; declivous face with strong transverse rugae. Middle and hind tibiae each with a single distinct apical spur. Wings slightly infuscated, marginal cell of fore-wing closed; hind wing with 6 - 8 hamuli.

Petiole about 1.6 times as long as wide, its sides slightly convex; anteriorly above with a few well-separated rugulae, with very short longitudinal rugulae along hind border. Postpetiole about 1.2 times longer than wide, free of sculpturing except for very short rugulae anteriorly and posteriorly. Abdomen subcylindrical; first tergite with fine short striae basally; remaining tergites smooth and shining, devoid of sculpturing. Genitalia and subgenital plate as illustrated.

Pubescence as described for *P. adlerzi* by Kempf (1958). Head, thorax, petiolar segments, and most of the first gastric tergite black; antennal scape fuscous-brown; funicular segments brown; legs reddish-brown, the tibiae lighter than the other segments; gastric segments brownish medially, lighter apically.

A male from colony No. 76513-2, collected at Cordoba, Veracruz, Mexico, July 13, 1965, by the author, has been selected as the andro-type and is deposited in the Los Angeles County Museum of Natural History.

At the time of my visit, *P. scabriusculus* was the most commonly encountered cephalotine; foraging (?) individuals were seen at dusk crawling up and down the trunks of the trees in which they nested. Of the six colonies taken, four appear to be complete; the two remaining were surely only frag-

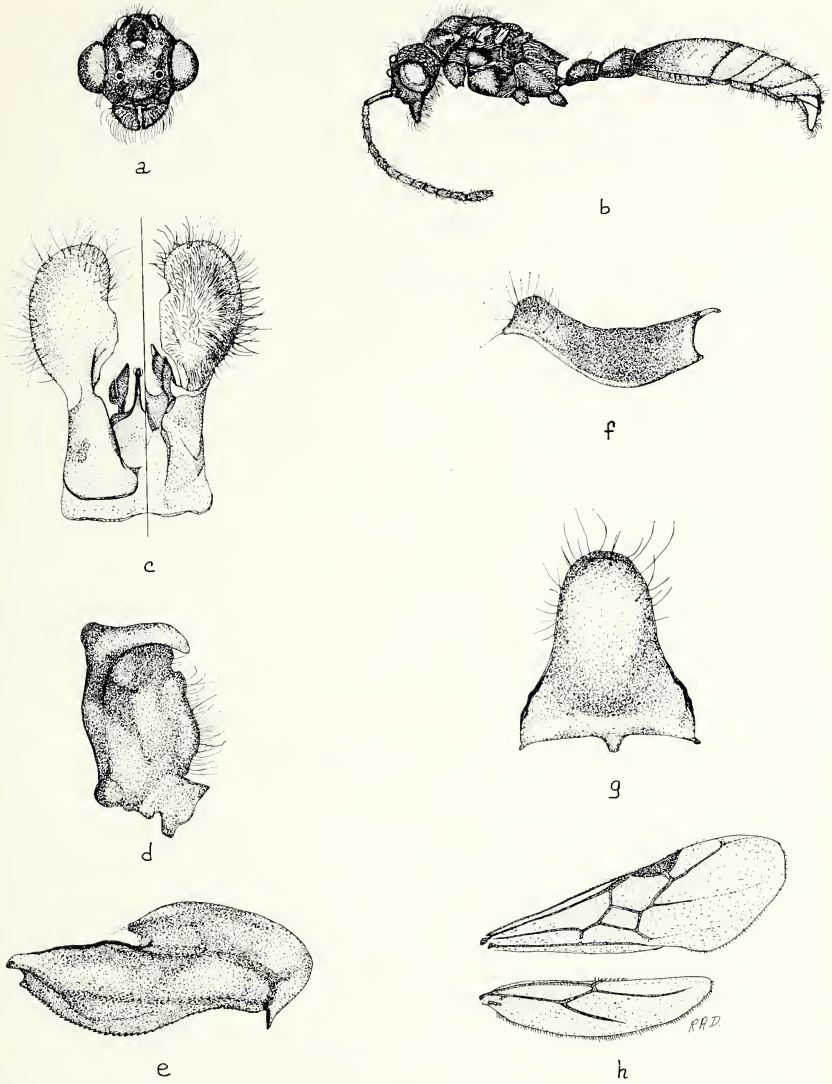



*Figure 1. Procryptocerus scabriusculus,* male: a, head; b, lateral aspect; c, genital capsule (left half, dorsal aspect; right half, ventral aspect without aedeagus); d, volsella, inner aspect; e, aedeagus, lateral aspect; f, subgenital plate, lateral aspect; g, subgenital plate, ventral aspect; h, fore and hind wings. Figures by Ruth DeNicola Snelling.

ments of a polydomous colony. All colonies were taken from dead twigs or limb stubs in living trees; none were found in the epiphyte samples which I examined, although *Cryptocerus* (*C.*) *multispinosus biguttatus* Emery was commonly found in such surroundings.

Foraging (?) individuals moved rather slowly, but when disturbed were capable of swift, agile movements for a short distance. Individuals of one colony (No. 76513-1) were seen on several occasions to move across the soil surface to another tree about seven feet from the nest tree. Although numerous presumed foragers were seen, none gave any clue as to the food habits. Twice, however, two different individuals accepted dead *Nasutitermes* workers; individuals regularly came to a honey-water mixture set out as bait.

On the evening of July 12, at 2045 hours, alate females from colony No. 76513-2 appeared and promptly took wing. Three males appeared at 2112 and remained on the stub for several minutes, showing no interest in the half dozen females nearby, which had emerged at 2105. The latter flew away at 2120, followed a few minutes later by the males. Two dealate females were taken the following night at 2203. A few workers were present on the stub at the same time as the sexual forms but did not pay them any attention. Shortly before the sexual phases appeared, a brief rain shower had thoroughly saturated the area; temperature was 72°F, humidity ca. 80-85%.

On several preceding nights, males were attracted to 15 watt ultraviolet "black light" tubes set up about 150 feet from the tree in which colony 76512-2 was located; unfortunately, the times at which these individuals arrived at the light source were not noted.

### **Cryptocerus (Cryptocerus) insularis** Wheeler, 1934

Figure 2

Wheeler (1934) described *C. pilosus insularis* on the basis of a single worker from Maria Madre Island (Tres Marias group), Nayarit, Mexico. Kempf (1958) showed that this ant was not allied to *C. pilosus* Emery, but belonged in his *rohweri*-subgroup, which also included *C. wheeleri*. Since the location of the unique type of *C. insularis* was unknown, he provisionally accorded it species status, but intimated it might prove to be either *C. rohweri* or *C. wheeleri*. *C. insularis* supposedly differed in the more prominent lateral pronotal teeth and the slightly emarginate anterior gastral border.

In 1964 I spent a day at the California Academy of Sciences, where the type evidently had been originally placed, in a futile effort to locate the missing type. In the Academy's type drawers is a unit tray with the original name of this ant, but no specimen. The type record carries the notation "type lost." A careful search through both the identified and unidentified formicid collections failed to produce the missing specimen. Since Kempf indicated that the type of *C. pilosus insularis* was not in the Wheeler Collection at the Museum of Comparative Zoology, it seems safe to assume that the specimen is no longer

extant. Accordingly, I have designated a NEOHOLOTYPE specimen from material at hand, and have selected a worker specimen taken on Maria Magdalena Island (Tres Marias group), Nayarit, March 25, 1964, ex colony No. 36425-c (R. R. Snelling)[2]. This specimen is deposited in the collections of the Los Angeles County Museum of Natural History.

Kempf (1958) separated the workers of *C. rohweri* and *C. wheeleri* as follows:

"Lower face of head longitudinally striato-rugose; frontal carinae testaceous and semitranslucid.....*wheeleri* Forel

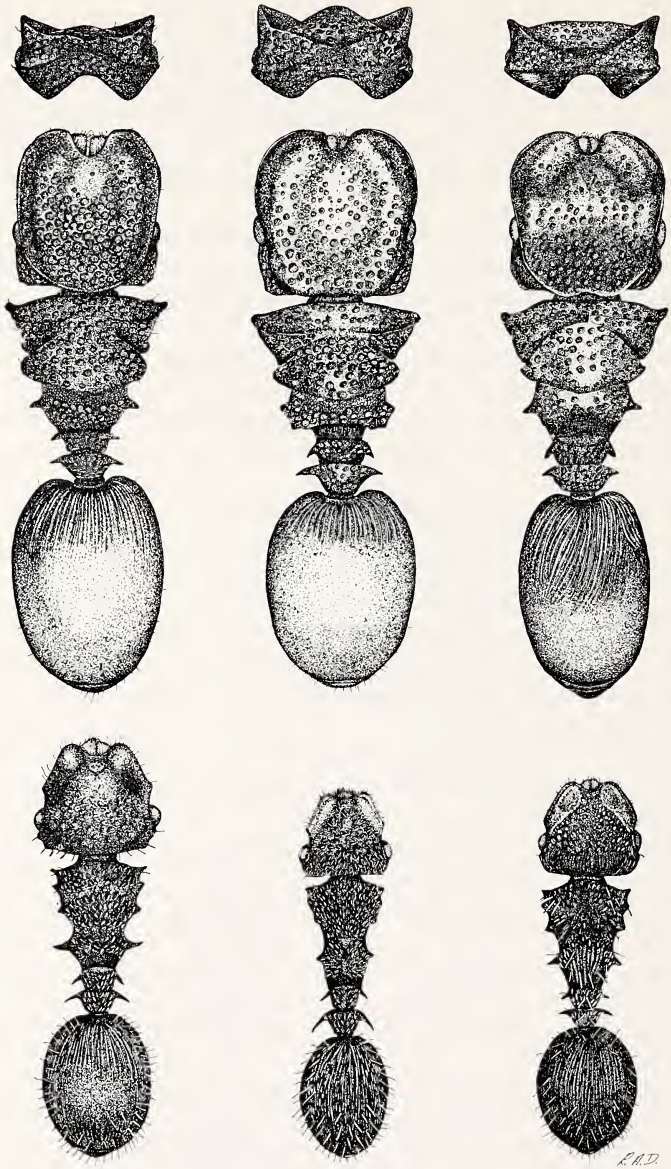
"Lower face of head reticulate-rugose; frontal carinae partly infuscated and solid.....*rohweri* Wheeler"

The workers of the insular form, when run through Kempf's key, will go directly to *C. wheeleri* with no difficulty. In his discussion of *C. wheeleri,* Kempf indicates additional characteristics by which the two species may be separated; the *C. insularis* workers differ from *C. rohweri* in exactly the same characters.

As pointed out above, Kempf allowed *C. insularis* to stand because of two apparently definitive characteristics which seemed to be at variance with the other species. The first of these is the more prominent lateral pronotal teeth. Wheeler, in his original description, stated that this form differs from ". . . typical *pilosus* in having the three lateral teeth of the pronotum longer and more acute." Wheeler based his concept of *C. pilosus,* specimens of which he had not seen, on Emery's description and figures of that species, and on a "related form" from Brazil. I must confess that I, too, have never seen *C. pilosus*; however, the normally excellent figures by Kempf should provide a good idea of the thoracic configuration. I have compared my material of *C. insularis* closely with Kempf's figures of *C. pilosus,* and fail to agree with Wheeler's claim. The anterior and middle lateral teeth in *C. insularis* exhibit some variation, but no individuals have these teeth any longer or more acute than the corresponding teeth in *C. pilosus*; if anything, they tend to be somewhat stouter. In many of the *C. insularis* workers the middle tooth is much reduced. The posterior tooth in the series before me is highly variable. It is safe to say, however, that on the whole it is better developed in *C. insularis* than in *C. pilosus,* if Kempf's figure may be considered to represent the average condition in that species.

Of the basal tergite Wheeler says "anterior border of the gaster at the articulation of the postpetiole less concave than in *C. pilosus* and without angular projections. . . ." In *C. pilosus* the first gastric segment at the articulation of the postpetiole is very decidedly concave, and on each side there are

[2]For the opportunity to collect ants on the Tres Marias Islands I am very deeply indebted to Mr. Richard F. Dwyer of Newport Beach, California. Mr. Dwyer provided transportation to the Islands aboard his vessel, then the "Gringa," now the "Sea Quest." To Mr. and Mrs. Dwyer and the crew of the "Gringa" my sincere thanks.



*rohweri* *insularis* *wheeleri*

*Figure 2. Cryptocerus* species, soldier (including dorsal aspect of head) and workers, respectively of *C. rohweri, C. insularis* and *C. wheeleri.* Figures by Ruth DeNicola Snelling.

strong angular projections. On the basis of this statement by Wheeler, Kempf evidently was led to expect at least some indication of such a concavity in *C. insularis*. It does exist, but certainly not to the degree that Wheeler's statement implied; the concavity, and it can barely be called that, is no more pronounced in my *C. insularis* samples than it is in *C. rohweri* or *C. wheeleri*.

The above discussion intends to show that the characters by which Kempf separated the three species in this complex are highly variable. This by no means, however, can be considered evidence that there are no good distinctions between them. If Wheeler's original description of *C. insularis* had been less vague, much of the difficulty which Kempf encountered could have been avoided.

Through the courtesy of M. R. Smith and D. L. Smith I have been able to examine the U. S. National Museum's material of *C. wheeleri*; Professor Creighton has sent me samples of *C. rohweri*. With these specimens, plus my material of *C. insularis*, it is now possible to restudy this complex and to affirm the specific nature of all three forms.

The majors of the three species present the most obvious and consistent distinction. That of *C. rohweri* differs from both *C. insularis* and *C. wheeleri* in the presence of a fringe of setae along the lower margins of the cephalic disc; no indication of this fringe is present in available material of the other two. Furthermore the major of the first species has coarser and more close-set foveolae on the cephalic disc; these foveolae, and the spaces between them, are distinctly granulose, and the foveolae lack flattened silvery hairs. Creighton (*in litt.*) has noted these distinctions between *C. rohweri* and *C. insularis*, and the cotypes of *C. wheeleri* available to me show they will separate the former from that species as well.

The floor of the cephalic disc is similarly shaped in *C. rohweri* and *C. insularis*; when viewed from directly above, it is strongly humped in the middle. In *C. wheeleri*, the disc is essentially flat all the way across when viewed in this manner. When the head of *C. rohweri* is viewed from the side, the rim of the cephalic disc appears much more pronounced above than in most majors of either of the other two species. One of our specimens of *C. insularis*, however, has the rim very nearly as well-developed as in *C. rohweri*. This same specimen, and one other from the same colony, has the cephalic foveolae nearly as large and close as they are in *C. rohweri*; but these foveolae all possess the flattened, shining hairs which are absent in *C. rohweri* and the interspaces are not granulose and dull as in that species.

In *C. wheeleri* the transverse pronotal carina is rather strongly humped on either side of the pronounced median excision. In *C. insularis* and *C. rohweri* the carina, when viewed from the front, is distinctly sinuate, but the median excision is barely detectable, and the carina is not humped on either side. In *C. rohweri* the lateral spines of the petiole and post-petiole are longer and sharper than in the other two species.

The integument of *C. rohweri,* including that of the cephalic and thoracic foveolae, is everywhere granulate, imparting to the entire insect a dull appearance which is not much offset by the few shining hairs in the thoracic foveolae. This is in rather strong contrast to the condition of both *C. insularis* and *C. wheeleri,* in which the integument, while tessellate between the foveolae, is not at all granulate and hence somewhat shining. In addition, each foveola possesses a shining, flattened hair at its bottom, imparting a further luster to the insect.

The minors are by no means as readily separable; differences do exist, but they are more subtle and, apparently, subject to greater variation. As is the case with the majors, the minors of *C. rohweri* differ from those of the other species in the more distinctly granulose integument. In this character, however, the distinction is one of degree, and accordingly difficult to appreciate unless all three species are available for comparison. However, in both *C. insularis* and *C. wheeleri,* the sides of the thorax and the posterior surface of the epinotum, while conspicuously tessellate, are nonetheless moderately shining; in *C. rohweri* these areas are granulate and dull. The gaster of the latter species is conspicuously duller than is the case with the other two. This is especially obvious along the sides of the first gastric tergite.

The underside of the head of *C. rohweri* is reticulate-rugose (as pointed out by Kempf), while in the other two species it is striato-rugose. Furthermore, in the latter two species the frontal carinae are testaceous and semitransluscent, while in *C. rohweri* they are somewhat thickened and partially infuscated.

The minor of *C. rohweri* is relatively easily separated from *C. insularis* and *C. wheeleri*; the latter two species, however, are less readily separated from one another. The two principal distinctions which I have noted, and which I use in the key below, are of questionable validity, since only two minors of *C. wheeleri* are available for study. In *C. insularis* the maximum head width, at the upper margin of the eyes, is slightly less than the maximum length, the mandibles excluded. The two cotypes of *C. wheeleri* both have the maximum head width slightly greater than the maximum head length. The longitudinal rugulae of the promesonotum of *C. insularis* are rather regularly spaced, and are basically parallel to one another, not noticeably convergent anteriorly. In *C. wheeleri,* on the other hand, these rugulae are irregularly spaced, not essentially parallel with one another, and are definitely convergent anteriorly.

The three species are allopatric in distribution: *C. rohweri* is known from the mountain ranges of southern Arizona and northwestern Mexico[3], *C. wheeleri* only from the types taken at Cuernavaca, Morelos, Mexico. *C. insularis* has been taken on the Tres Marias Islands, Nayarit, and on the coastal lowlands near Mazatlan, Sinaloa, Mexico.

[3]The presence of this species in Mexico is indicated by a single female taken 13.6 miles west of Alamos, Sonora, on July 17, 1963 by R. L. Westcott.

I consider the two specimens taken in quarantine and recorded by Kempf (1958: 134) as *C. wheeleri* to be examples of *C. insularis*; both were from unknown localities in Mexico. These two specimens have been examined and compared with my material of *C. insularis,* with which they agree quite closely. In all the characters discussed above, they coincide with *C. insularis* rather than *C. wheeleri.* The removal of these specimens from the records of *C. wheeleri* leaves only the original type series to represent that poorly known species.

The following key is intended to supplement that of Kempf (1958) in securing separations of the three species involved, since he was unable to include *C. insularis.*

## KEY TO MEMBERS OF **CRYPTOCERUS WHEELERI** COMPLEX

1. Majors ..... 2
   Minors ..... 4

2. Lateral projecting lobe of mesonotum angulate or dentate; rim of cephalic disc without projecting setae..... 3
   Lateral projecting lobe of mesonotum broadly rounded, not angulate or dentate; rim of cephalic disc with fringe of projecting setae..... .....*C. rohweri* Wheeler

3. Seen from above, floor of cephalic disc strongly humped in middle; transverse pronotal carina lacking distinct median excision..... .....*C. insularis* Wheeler
   Seen from above, floor of cephalic disc flat, not at all humped in middle; transverse pronotal carina sharp, strongly excised medially..... .....*C. wheeleri* Forel

4. Genal area longitudinally striato-rugose; frontal carinae testaceous and semitransluscent ..... 5
   Genal area reticulate-rugose; frontal carinae thickened, partly infuscated.....*C. rohweri* Wheeler

5. Maximum head width, at upper margin of eyes, slightly less than maximum length (mandibles excluded); rugulae of promesonotum regularly spaced, parallel, not convergent anteromedially.....*C. insularis* Wheeler
   Maximum head width slightly greater than greatest length (mandibles excluded); rugulae of promesonotum more irregular, not essentially parallel, distinctly convergent toward anterior middle.....*C. wheeleri* Forel

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*By* WILLIAM A. CLEMENS, JR.

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DOROTHY M. HALMOS
*Editor*

# A MANDIBLE OF *DIDELPHODON VORAX* (MARSUPIALIA, MAMMALIA)

*By* William A. Clemens, Jr.[1]

Abstract: A fragment of a mandible of *Didelphodon vorax* found in the Hell Creek Formation, Montana, confirms the provisional identification of lower premolars and molars of this species, establishes the orientation of the lower premolars, and serves as the basis for further speculation on the orientation of the upper premolars. The functional significance of prominent lateral lobes on mammalian premolars is examined.

## Introduction

*Didelphodon* is the largest of the Late Cretaceous marsupials and probably the largest mammal known from any Mesozoic fauna. In addition to its size, the striking modifications of its dentition raise questions concerning the role of *Didelphodon* in the reptile-dominated terrestrial environments of the Cretaceous. When I prepared my study of the marsupials of the Late Cretaceous Lance local fauna (Clemens, 1966), approximately 200 isolated teeth but only seven mandibular fragments of *D. vorax* were available for study. None of these mandibular fragments is as complete as that included in the type of *Didelphodon padanicus* from Late Cretaceous deposits in South Dakota, which contains only two undamaged although heavily worn teeth, the posterior premolar and a questionably associated molar. Also available for comparison is a fragment of an edentulous mandible from the Hell Creek Formation that has been described by Simpson (1927) and can be provisionally identified as representing a species of this genus. The fossil found in the Hell Creek Formation and described in this paper is the most nearly complete mandible of *Didelphodon* yet discovered. It provides significant information correcting and extending previous restorations of the mandible and dentition of *Didelphodon*.

## Acknowledgments

The mandible of *Didelphodon* described here was found by Mr. Harley J. Garbani, a member of a field party from the Los Angeles County Museum of Natural History that collected fossil vertebrates from the Hell Creek Formation of Montana in the summer of 1965. This work was made possible by a generous gift from Mr. and Mrs. William T. Sesnon, Jr. I am greatly indebted to Dr. J. R. Macdonald of the Los Angeles County Museum of Natural History (LACM) who made the fossil available to me for study.

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My research is part of a study of North American Late Cretaceous mammals supported by a grant from the National Science Foundation (GB-5121) and the Museum of Natural History of the University of Kansas. The illustrations were prepared by Mr. Merton Bowman, to whom I am particularly indebted for help with the restoration of the mandible.

I also express my thanks to the following individuals and institutions for the opportunity to study materials in their care: Donald E. Savage, Museum of Paleontology, University of California, Berkeley (UCMP); Seth B. Benson, Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); J. Knox Jones, Museum of Natural History, University of Kansas (KU); Donald E. Russell, Institut de Paléontologie, Paris; and to Jason A. Lillegraven for his constructive criticism of the manuscript.

## MATERIAL

*Locality*: Dr. J. R. Macdonald provided the following information: *Lower Hell Creek no. 1.* Late Cretaceous. Hell Creek Formation. In purple to gray clay and sandy silt, crusty brownish-gray with yellow and brown spots, also some medium-size, round sand concretions and carbonized wood resembling charcoal. Maloney Hill Quadrangle, Garfield County, Montana. Additional locality data are on file at the Los Angeles County Museum of Natural History and available to qualified investigators.

*Description*: The fossil (LACM 15433) is a fragment of a left mandibular ramus lacking that part of the symphyseal region anterior to the canine. Posteriorly it is broken at the level of the anterior edge of the coronoid process. The root of the canine and alveoli of $P_1$ are present. $P_2$, its apex slightly blunted by wear, and $P_3$, which shows less wear, are preserved. $M_{1-2}$ are missing but $M_3$, which has large wear facets on the trigonid and talonid, is preserved. Only the trigonid of $M_4$, less worn than that of $M_3$, remains. The symphysis extends posteriorly to a point below the anterior edge of $P_3$. Two mental foramina are present, one below $P_{2-3}$, the other below $M_{1-2}$. Measurements of the fossil are given in Table 1.

TABLE 1
Measurements of LACM 15433 in millimeters

Dentition

| | $P_2$ | $P_3$ | $M_3$ | | | $M_4$ |
|---|---|---|---|---|---|---|
| Length | 6.5 | 7.3 | 6.5 | | | —— |
| Width | 5.4 | 4.8 | 4.8 | (trigonid) | 4.5 (talonid) | 5.4 (trigonid) |

Dentary

| | Below $P_3$ | Below $M_3$ |
|---|---|---|
| Height | 14.7 | ca. 19. |
| Width | 8.6 | ca. 8. |

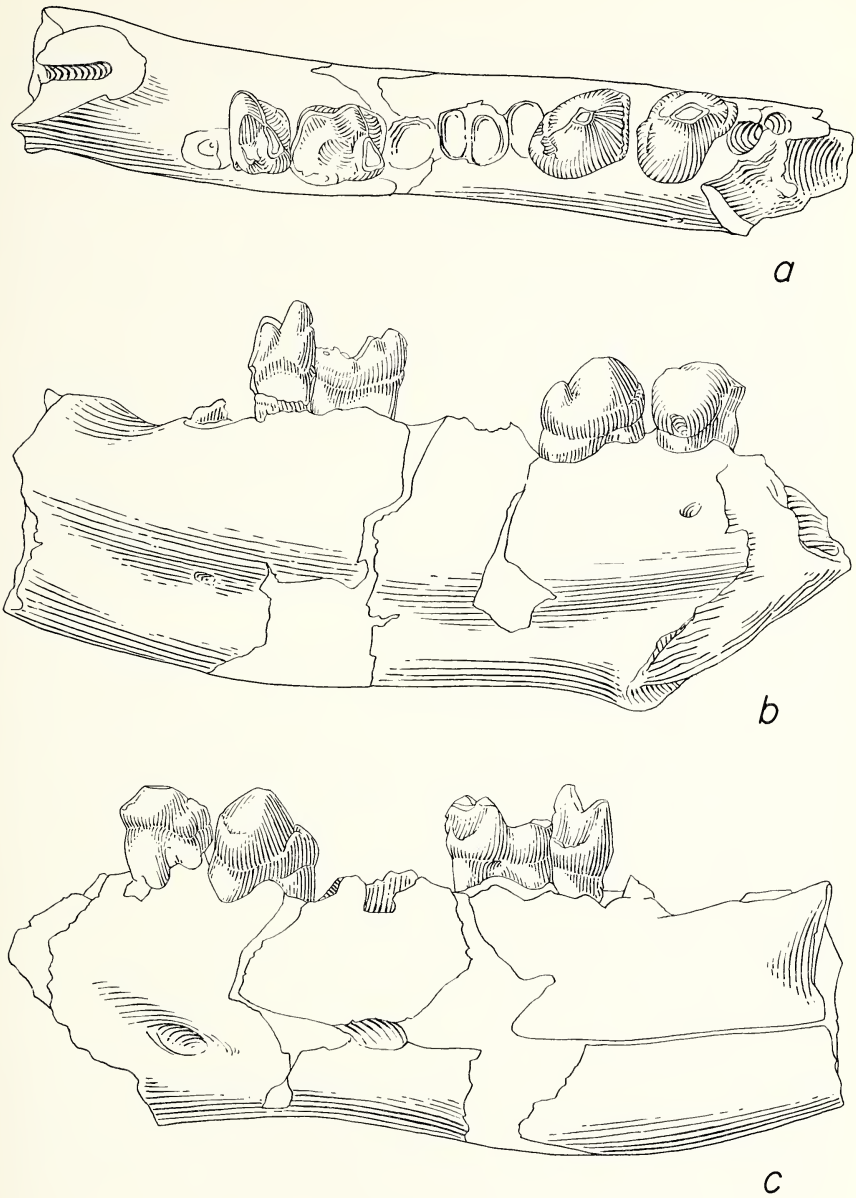


*Figure 1. Didelphodon vorax,* LACM 15433: left mandibular ramus with $P_{2\text{-}3}$, $M_3$, and trignoid of $M_4$ preserved; *a,* occlusal; *b,* lingual; and *c,* labial views; all X 2.

## COMMENTS

In my review of the marsupials of the Lance Formation (Clemens, 1966), two species of *Didelphodon,* the type species *D. padanicus* and *D. vorax,* were recognized. Fossils from the Lance Creek area demonstrate *D. vorax* has three lower premolars of which $P_1$ is the smallest and $P_3$ the largest. The evidence afforded by the only known mandible of *D. padanicus* does not clearly document its premolar structure. What remains of the premolars indicates the presence of either four premolars or three premolars with the second being distinctly larger than the last. Differences between species were also observed in morphology of the presumed posterior upper premolars and, possibly, in the smaller size of the teeth of *D. vorax.*

The premolar morphology of LACM 15433 is of the type characteristic of *Didelphodon vorax.* Only three premolars are present. $P_2$ is smaller than $P_3$, although the difference is not so large as would be expected from the isolated teeth in the sample of the Lance local fauna. In only one of its dental dimensions (width of $P_2$) does the fossil exceed the observed ranges of variation of the Lance sample. The characters of the molars and dentary also support allocation of the fossil to the species *D. vorax.* This discovery extends the range of the species to include the Hell Creek Formation of eastern Montana.

## RESTORATION OF THE DENTITION

LACM 15433 permits confirmation of some points in my study (Clemens, 1966) of the lower dentition of *Didelphodon vorax.* These can be summarized as follows: Association of the lower molars and premolars provisionally allocated to *D. vorax* is now demonstrated. The lateral lobes of $P_2$ and, no doubt, $P_1$ are on the lingual sides of their crowns. The trigonid of $M_1$ is labial to the posterior end of $P_3$. Although the evidence is still not conclusive, the lower molars appear to have increased in size from $M_1$, the smallest, to $M_4$. The observed range of the ratios of widths of trigonid/talonid derived from isolated teeth in the Lance sample thought to be $M_3$'s, 1.07 to 1.13, includes the value of the ratio, 1.07, for the $M_3$ in LACM 15433.

Using LACM 15433 as a base and selecting teeth collected from the Lance Formation to replace those postcanine teeth missing from it, a partial restoration of the mandible (Fig. 2) has been prepared. The restoration of the canine is based on canines of *Sarcophilus,* and a large isolated canine, YPM 10667, from the Lance Formation described by Marsh (1892, Pl. VIII, fig. 6) and tentatively referred to *Didelphodon vorax.*

In my earlier paper an attempt was made to determine the orientation of the upper premolars of *Didelphodon vorax,* which are known only from isolated teeth. Because of the morphology and apparently regular pattern

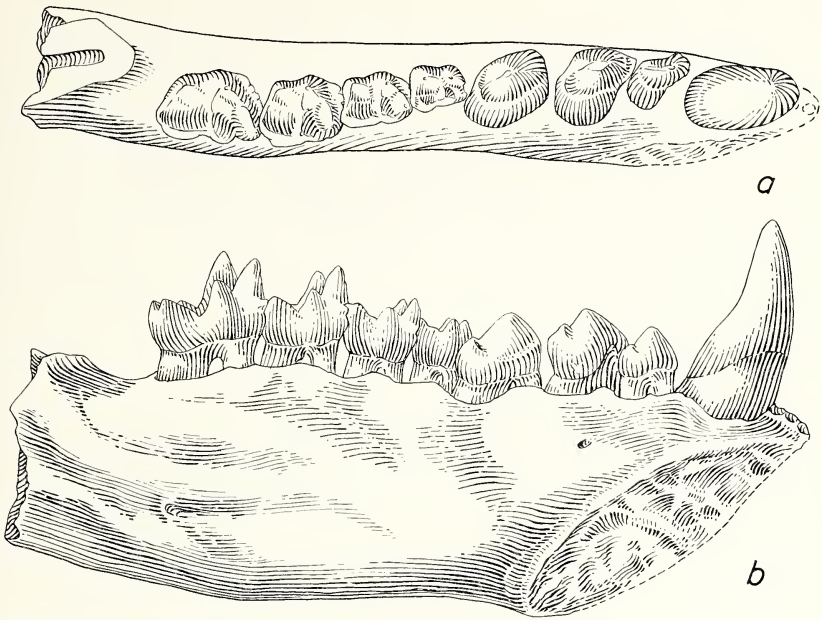


*Figure 2. Didelphodon vorax*; partial restoration of left mandible; *a*, occlusal, and *b*, lingual views; both X 1.8.

and sequence in development of wear facets on these teeth, it was assumed the entire battery of lower premolars made contact with the upper premolars. Orientation of the lower premolars with their lobes on the lingual sides of the teeth was supported by some evidence. From study of the wear patterns it appeared to follow that the upper premolars were oriented with the lobes on their labial sides. The orientation was also supported by consideration of the general pattern of symmetry of mammalian dentitions. Although not fully disproving the proposed orientation, several points have come to my attention suggesting that the reverse orientation—the lobes of the upper premolars on the lingual sides of their crowns—is probably correct.

The first restoration of the upper premolars of *Didelphodon* was proposed with the implicit assumption that development of prominent lateral lobes of $P_{1-2}^{1-2}$ was the result of selection for increase in the area of contact of the upper and lower premolars. Information obtained from a large series of skulls of *Sarcophilus* (in the Museum of Vertebrate Zoology) supports an alternative assumption.

In gross morphology the lower premolars of *Sarcophilus* (Fig. 3) resemble those of *Didelphodon* and show the same pattern of wear. The

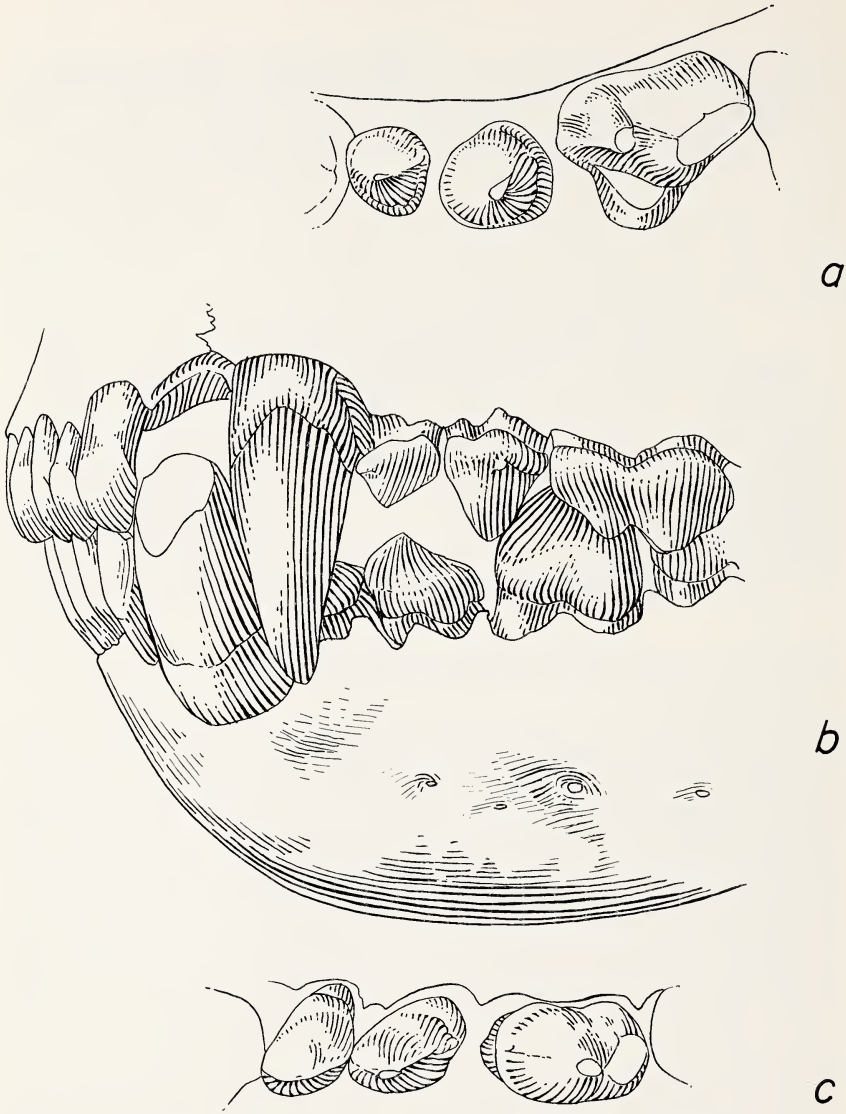


*Figure 3. Sarcophilus harrisi*, MVZ 127035: *a*, occlusal view, $P^{1-2}$ and $M^1$; *b*, lateral view of left upper and lower incisors, canines, premolars, $M\frac{1}{1}$, and part of $M_2$; *c*, occlusal view, $P_{1-2}$ and $M_1$; all X 2.25.

lower premolars of *Sarcophilus* do not contact the uppers when the molars are occluded. $P^2$ lacks a lobe on the lingual side of its crown. This premolar is situated with the long axis of its crown forming an oblique angle with the midline of the palate and, when the molars are occluded, it lies close to the crown of $M_1$. In contrast, in those dentitions of *Sarcophilus* studied, a few $P^1$'s have a small lingual lobe, but most $P^1$'s resemble the tooth illustrated here (Fig. 3), which has only a small lingual expansion bordered by a prominent cingulum. Because this cingulum is well removed from the apex of the crown of $P_2$ when the molars are occluded, it cannot act to increase the area of contact of the upper and lower dentitions.

The convex sides of brachyodont mammalian cheek teeth serve to protect the margin of the gingiva from damage through direct contact with hard or abrasive materials. Because the upper and lower premolars of *Sarcophilus* do not come into contact during occlusion of the molars, development of lobes and cingula on their crowns cannot be attributed to selection for increase of the occlusal area. The modifications probably were developed in response to selection for increase of the area protected by the premolar crowns or change in configuration of the crown to protect the margin of the gingiva.

Similarity in premolar morphology and wear patterns of *Sarcophilus* and *Didelphodon* suggests the assumption that $P_{1-2}$ of *Didelphodon* occluded with $P^{1-2}$ could be erroneous. If these premolars of *D. vorax* did not occlude, the function of their lateral lobes could have been to provide protection for the gingiva, and lobes on the upper premolars could have been on the lingual sides of their crowns. This function and orientation is favored by the presence of steeply inclined wear facets on the lobes of some premolars that might not have developed through contact of upper and lower premolars.

Many extant mammals have premolars with bulbous crowns and, less frequently, lateral expansions or lobes. Restricting comparisons to mammals of approximately the same size—as far as can be determined from mandibular dimensions—the closest resemblance in dental morphology to *Didelphodon* is found in *Sarcophilus* and it is not close. Although the molars (Fig. 4) of the sea otter, *Enhydra,* and *Didelphodon* are distinctly different in function and morphology, their premolars show points of resemblance. The upper and lower first premolars of *Enhydra* usually are lost, but a small peglike $P^1$ is present in either the upper right or left quadrant of some dentitions (2 of 12 individuals represented in the University of Kansas collections). $P_2$ and $P_3$, which do not occlude with upper premolars, have prominent lobes on the lingual sides of their crowns. The small lobe on the lingual side of $P^2$ is dorsal to but does not occlude with $P_3$. The lobe on the lingual side of $P^3$ is larger than that of $P^2$ and has a shallow basin on its surface that receives the apex of $P_4$.

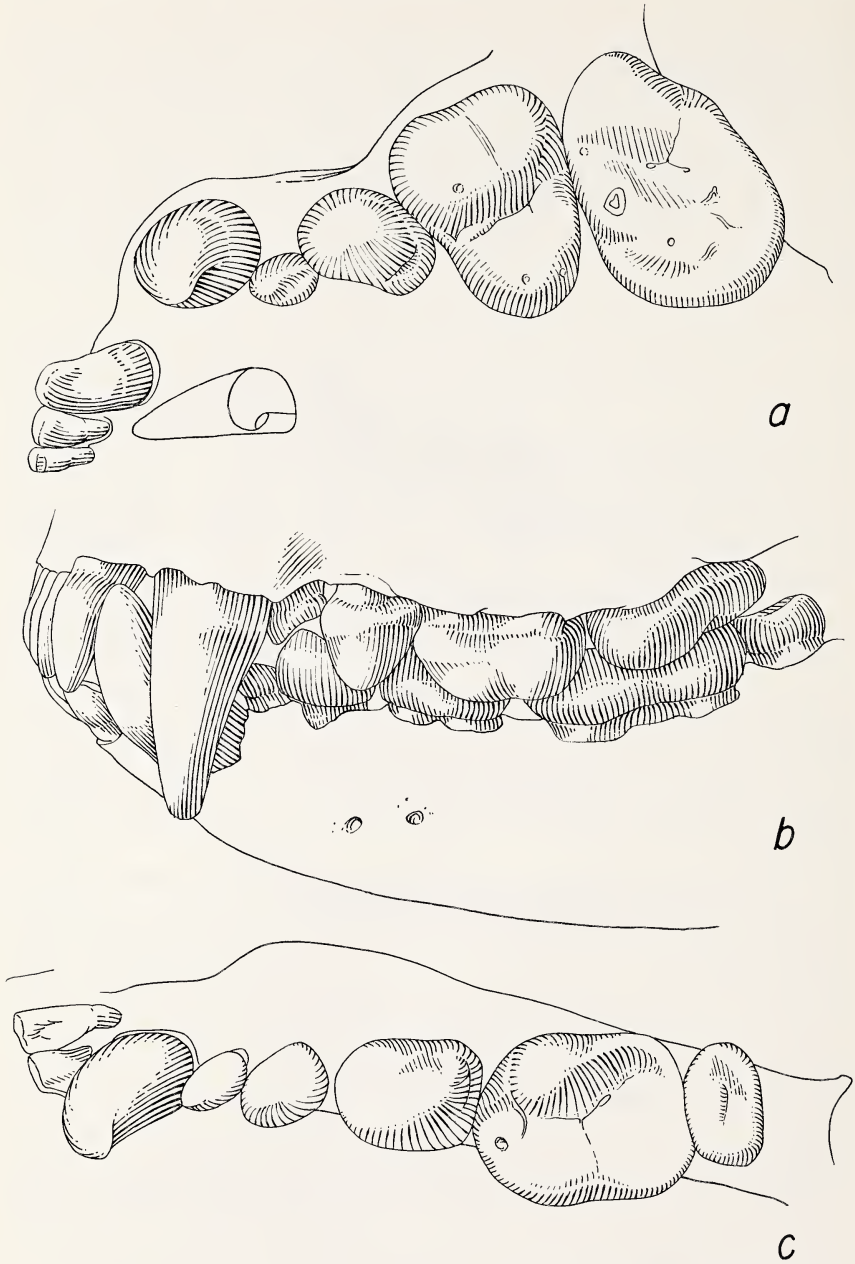


*Figure 4. Enhydra lutris*, KU 44672: *a*, occlusal view, $P^{2-4}$ and $M^1$; *b*, lateral view of entire dentition; *c*, occlusal view, $P_{2-4}$, $M_{1-2}$; all X 2.17.

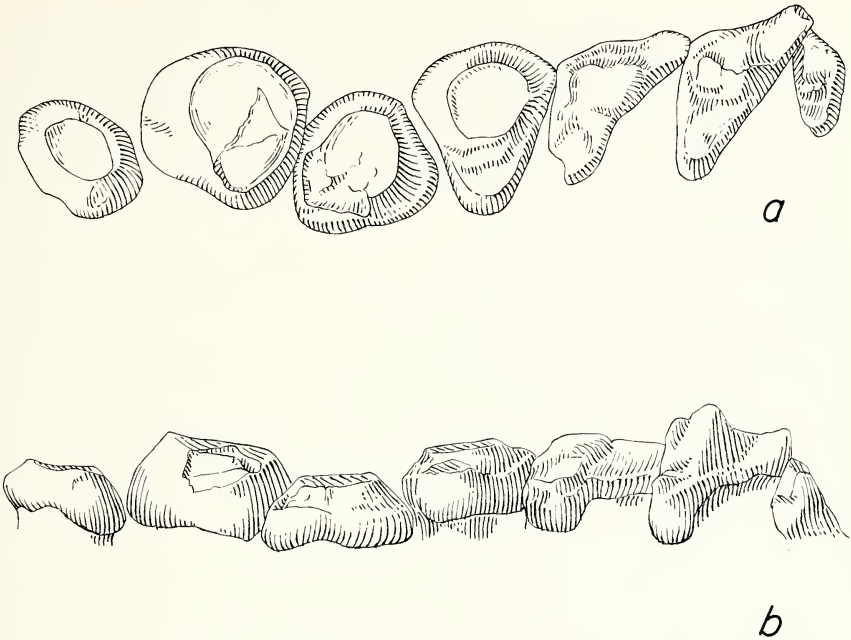


*Figure 5. Quercitherium tenebrosum,* Collections de Paléontologie, Muséum national d'Histoire naturelle, 1893-11: left maxillary fragment with $P^{1-4}$ and $M^{1-3}$; illustrations based on figures in Piveteau (1935) and cast of fossil; *a,* occlusal, and *b,* lingual views; both approximately X 2.

Comparisons can be carried further among placental mammals. The recently established oxyaenoid family, Teratodontidae Savage, 1965, is composed of *Teratodon* and *Quercitherium.* Both have dentitions resembling the dentition of *Didelphodon* in the presence of massive premolars and some shearing molars. Apparently in one species, *Teratodon enigmae,* the first molars also have greatly modified, bulbous crowns. The bulbous teeth of *Teratodon* do not have the prominent lobes found in *Didelphodon.* Savage (1965: 252) suggests the upper and lower premolars of *Teratodon* occluded and were employed in a grinding action.

With the exception of $P^1$, which has a lingual lobe, the premolars of *Quercitherium* (Fig. 5) more closely resemble those of *Teratodon* than *Didelphodon.* The available casts and illustrations do not reveal whether the wear facets on the premolars of *Quercitherium* are the result of occlusion or apical, non-occlusal wear of the type described by Mac Intyre (1966: 123). However, its position relative to the crowns of other premolars suggests the lingual lobe of $P^1$ functioned to protect the gingiva.

Because of their position relative to the insertion of the masseter and

the condyle, the massive premolars of *Teratodon* would have obtained little mechanical advantage from the leverage of the mandibular ramus. Savage (1965) noted that functionally the dentition appears to be a compromise between shearing and crushing or grinding functions but one bringing out the worst attributes of both. In teratodontids and *Didelphodon* the lack of great mechanical advantage for the premolars could have been offset by the evolution of a massive masticatory musculature. This modification is found in the jaw musculature of *Sarcophilus*. As Macalister (1872: 18) noted, "The most expressive way of representing the enormous size of these muscles [of *Sarcophilus*] is by stating that the weights of the muscles which elevate the lower jaw (masseters, pterygoids, and temporals) were equal to the sum of the weights of all the scapular and brachial muscles (deltoids, spinates, biceps, brachiales, triceps, & c.), or to the entire series of muscles which act on the shoulder-joint (pectorals, latissimus dorsi, spinati, deltoids, & c.)."

Data obtained from mammals with premolars resembling those of *Didelphodon* suggest the following points concerning the function and orientation of this kind of premolar: Evolution of lateral lobes need not be a response to selection for increase of the occlusal area of the dentition, but may serve to change the configuration of the margin of the gingiva to give it greater protection or increase the area protected by the crowns of the premolars. Presence of these lobes does not necessarily indicate the opposing upper and lower premolars occluded. In all species in which the orientation of the teeth can be definitely established, the lobes are found only on the lingual sides of the upper and lower premolars.

## SUMMARY

A fragment of a mandible of *Didelphodon vorax* found in the Hell Creek Formation is described and used as the basis for a restoration of the lower dentition of the species. The morphology of the teeth preserved in this mandibular fragment and evidence from other sources suggests the previously proposed orientation of the upper premolars was erroneous. Prominent lobes on some premolars of *Didelphodon* probably result from selection for increase of the area protected by the premolars or changes in configuration of the crown to protect the margin of the gingiva, not from selection for increase in the area of contact of the upper and lower premolars. Although not fully demonstrated, it now appears most likely that, like the lobes on the lower premolars, those on the upper premolars were also on the lingual sides of their crowns.

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*By* ROY W. MCDIARMID

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DOROTHY M. HALMOS
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# POPULATIONAL VARIATION IN THE FROG GENUS *PHRYNOHYAS* FITZINGER IN MIDDLE AMERICA

*By* Roy W. McDiarmid[1]

Abstract: A detailed populational analysis indicates that *Phrynohyas latifasciata, inflata,* and *spilomma* are all representative of a single wide-ranging form, *Phrynohyas venulosa.* Important characteristics, including size, coloration, and skin texture, exhibit considerable variation and extensive overlap from population to population or within the same population.

The largest specimens of *Phrynohyas* occur in the more arid portions of its range. Large size is considered an important mechanism for increasing the frogs' efficiency in unfavorable habitats and allowing them to cope more effectively with the problems of desiccation. The degree of development of the dermal glands correlates with the annual climatic cycle characteristic of the wet and dry seasons in Costa Rica. Glandular secretions of *Phrynohyas venulosa* are considered a secondary adaptation against desiccation, as well as being important in deterring predators.

During the summer months of 1962, a field party from the University of Southern California conducted an extensive survey of the lowland amphibian and reptilian faunas of northwestern Mexico. On August 3 a series of nine large hylid frogs, genus *Phrynohyas,* was obtained from a rain-filled pond approximately 9 miles south of Escuinapa, Sinaloa. The frogs, eight males and one female, were located by their calls. Apparently this species was just initiating breeding activities, as only one pair was in amplexus. A second series of these frogs was collected on July 1 in Nayarit by a field party from California State College at Long Beach. This second series, 18 males and one female, was located by the loud chorus at a pond situated 0.1 mile west of the junction of Mexico Highway 15 and Highway 46, in Nayarit.

For the past eight years field parties from the University of Southern California have collected amphibians and reptiles in Costa Rica. In 1964, 1966, and again in 1967, I collected specimens of *Phrynohyas* in Guanacaste and Puntarenas Provinces of Costa Rica. Several of these specimens show striking similarities, particularly in color pattern, to specimens from western Mexico.

The results of a preliminary examination of the two series from Sinaloa and Nayarit indicate the need for a re-evaluation of the present understanding of the systematic arrangement of the genus in western Mexico. Also, with the availability of this additional material from Costa Rica, it seems appropriate to attempt to elucidate the relationships among the named populations of *Phrynohyas* in Middle America.

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## HISTORICAL REVIEW

As Duellman (1956), in a monograph on the genus *Phrynohyas*, presented an historical account that included complete synonomies and literature references for each species, a review of material published prior to 1956 will not be repeated. Duellman (1956:8) proposed that *Phrynohyas* be used to refer to those frogs that possess "paired lateral vocal sacs behind the angles of the jaws and without the skin of the head co-ossified with the skull." The generic name *Phrynohyas* was adopted and, following Opinion 520 of the International Commission on Zoological Nomenclature (Hemming, 1958), has been used by most authors (Gans, 1960; Porter, 1962; Stuart, 1963; Zweifel, 1964; Savage, 1966). Rivero (1961:128-131) discussed Duellman's proposal at some length and presented an alternative for treatment of frogs referred to *Phrynohyas*. He suggested that the species be maintained in the genus *Hyla* (see Rivero, 1961, for additional discussion).

On the basis of the unique characters of the larvae of *Phrynohyas* (Zweifel, 1964:204-205) and the characters used by Duellman to diagnose this group of frogs, it seems reasonable to maintain the generic name *Phrynohyas*. For the sake of nomenclatural stability, in accordance with Opinion 520, those frogs referred to *Phrynohyas zonata* (Spix) by Duellman (1956), and to *Hyla tibiatrix* Laurenti by Rivero (1961), are assigned to *Phrynohyas venulosa* (Laurenti).

The five species of Middle American *Phrynohyas* recognized by Duellman (1956) are: *P. zonata* from Costa Rica, Panamá, and tropical South America; *P. spilomma* from southern Tamaulipas, Mexico, southward along the eastern coast of Central America to Nicaragua and along the Pacific coast from the Isthmus of Tehuantepec southward to Guatemala; *P. modesta* from El Salvador north along the Pacific coast of Chiapas through the region of the Isthmus of Tehuantepec into the Atlantic drainage; *P. inflata* from scattered localities along the Pacific coast of Mexico from central Guerrero north to Colima; and *P. latifasciata* from Presidio, Sinaloa, Mexico.

Shannon and Humphrey (1957) described *Phrynohyas corasterias* from a single young female collected 4.8 miles east of San Blas, Nayarit. This species was diagnosed on the basis of pattern and coloration. The only known specimen of *P. corasterias* was collected from a locality approximately midway between the northernmost locality for *P. inflata* and the type locality of *P. latifasciata*. Duellman (1961:45-46) discussed the characters used to diagnose *P. corasterias* and placed it in synonomy with *P. inflata*. He suggested that additional material from northwestern Mexico might show that *P. inflata* and *P. latifasciata* are conspecific (Duellman, 1956:21; 1961:45).

Examination of additional material from Guatemala convinced Duellman that the uniform brown or tan dorsum characteristic of *P. modesta* is only a color variant of *P. spilomma*, and accordingly he placed *P. modesta* in the synonomy of *P. spilomma* (Duellman, 1966:277).

## METHODS AND MATERIALS

As presently understood, the species of *Phrynohyas* are distinguished by differences in size, body proportions, coloration, and pattern. To supplement the data gathered by Duellman from more than 350 specimens, I examined an additional 153 specimens of *Phrynohyas* from localities in western Mexico, Guatemala, Honduras, Costa Rica, and Panamá. Seven measurements, including body length, tibia length, foot length, head width, head length, interorbital distance, and internarial distance, were taken on each suitable specimen; five proportions were calculated from these measurements. These data are contained in Table 1. In order to standardize the measurements, only specimens larger than 45 mm in body length and capable of breeding are included. This procedure reduces the possibility of allometric growth in subadult stages confusing the data. The measurements taken are the same as those used by Duellman (1956:6-7). All measurements are in millimeters and were made with Helios dial calipers. Each available specimen was examined in detail with reference to skin texture, coloration, and pattern, because these characters, as presently understood, are the primary features used to distinguish between the species (see key to adult *Phrynohyas* in Duellman, 1956:43-44).

## ANALYSIS OF THE POPULATIONS

*Western Mexico.*—The northernmost representatives of the genus were collected at Presidio, Sinaloa (Boulenger, 1882). Examination of these two specimens led Duellman (1956:24-25) to describe *P. latifasciata.* The Sinaloan species was described as being most closely related to *P. inflata,* a species known from six males collected from localities in Colima, Michoacán, and Guerrero to the south. The characters he used to distinguish between *P. latifasciata* and *P. inflata* were differences in size, skin texture, coloration, and pattern.

The utilization of size in diagnosing a species of frog known from only two specimens is open to criticism. Furthermore, in the case of *P. latifasciata,* there is no mention of the time of year the frogs were collected nor of the breeding condition of the specimens. The paratype of *P. latifasciata* is a young specimen. If it was collected at the same time as the holotype, as presumed by Duellman (1956:24), then I suspect that the specimens were taken before the breeding season. The holotype may be an adult, but if it is sexually mature, it probably is a young adult. This supposition is supported by the size range of males taken less than 50 miles to the south of the type locality (Table 1). At this locale, breeding males measuring from 74.2 to 90.2 mm were collected. In addition, a male (UMMZ 108019) referred to *P. inflata,* measures 63.5 mm, approximately 5 mm less than the type of *latifasciata.* The size of the vocal sacs as depicted in the illustration of the holotype of *P. latifasciata* (Duellman, 1956:pl. III, fig. 1), when compared to those of breeding males from Sinaloa

## TABLE 1

### Measurements and Proportion

| | *P. latifasciata*[1] | | Sinaloa | | Nayarit | | Colima-Guerrero | | Oaxaca-Veracru | |
|---|---|---|---|---|---|---|---|---|---|---|
| | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀ |
| Number of Specimens | 1 | 0 | 6 | 1 | 17 | 1 | 5 | 0 | 4 | |
| Body Length mm | | | | | | | | | | |
| mean | — | — | 80.9 | — | 84.9 | — | 80.3 | — | 65.6 | 5 |
| range | 68.0 | — | 74.2-90.2 | 89.0 | 81.1-92.6 | 95.8 | 63.5-92.0 | — | 55.9-69.0 | 47.4 |
| Tibia Length mm | | | | | | | | | | |
| mean | — | — | 35.7 | — | 39.7 | — | 34.5 | — | 30.3 | 2 |
| range | 30.0 | — | 33.5-39.3 | 39.5 | 37.9-42.8 | 42.9 | 32.0-42.0 | — | 26.0-33.0 | 24.1 |
| Foot Length mm | | | | | | | | | | |
| mean | — | — | 32.1 | — | 35.0 | — | 29.7 | — | 24.4 | 2 |
| range | 28.5 | — | 30.0-35.1 | 35.5 | 31.0-37.1 | 40.1 | 26.0-32.0 | — | 21.2-26.0 | 19.4 |
| Head Length mm | | | | | | | | | | |
| mean | — | — | 23.8 | — | 25.0 | — | 23.6 | — | 19.5 | 1 |
| range | 20.5 | — | 22.5-26.2 | 25.7 | 23.0-26.6 | 28.1 | 20.0-27.0 | — | 15.8-21.0 | 15.4 |
| Head Width mm | | | | | | | | | | |
| mean | — | — | 25.8 | — | 27.0 | — | 26.0 | — | 20.5 | 1 |
| range | 22.0 | — | 24.0-27.8 | 28.5 | 26.0-28.2 | 30.5 | 21.0-29.0 | — | 16.5-23.0 | 15.8 |
| Interorbital Distance mm | | | | | | | | | | |
| mean | — | — | 7.5 | — | 7.8 | — | 7.5 | — | 5.7 | |
| range | 6.0 | — | 6.9-8.2 | 9.5 | 7.0-9.4 | 8.8 | 5.5-9.0 | — | 4.6-7.0 | 5.1 |
| Internarial Distance mm | | | | | | | | | | |
| mean | — | — | 5.6 | — | 6.2 | — | 6.2 | — | 4.9 | 4 |
| range | 4.0 | — | 4.9-6.1 | 6.2 | 5.5-6.7 | 6.5 | 5.5-7.0 | — | 4.1-6.0 | 3.9 |
| % Tibia Length/Body Length | | | | | | | | | | |
| mean | — | — | 44.2 | — | 46.8 | — | 47.6 | — | 46.2 | 4 |
| range | 44.1 | — | 42.5-45.6 | 44.4 | 44.6-48.4 | 44.8 | 45.6-50.7 | — | 44.1-47.8 | 49.1 |
| % Head Length/Body Length | | | | | | | | | | |
| mean | — | — | 29.5 | — | 29.4 | — | 32.5 | — | 29.6 | 3 |
| range | 30.1 | — | 27.6-31.5 | 28.8 | 28.0-31.3 | 29.3 | 31.5-33.3 | — | 28.3-30.4 | 32.8 |
| % Head Width/Body Length | | | | | | | | | | |
| mean | — | — | 32.0 | — | 31.8 | — | 29.6 | — | 31.1 | 3 |
| range | 32.3 | — | 30.3-33.5 | 32.0 | 29.4-35.0 | 31.8 | 27.7-31.5 | — | 29.2-33.3 | 31.0 |
| % Interorbital Distance/ Head Width | | | | | | | | | | |
| mean | — | — | 29.0 | — | 28.9 | — | 28.7 | — | 28.0 | 3 |
| range | 27.3 | — | 27.0-31.2 | 33.3 | 25.8-33.3 | 28.8 | 26.2-31.0 | — | 26.1-31.1 | 28.2 |
| % Internarial Distance/ Head Width | | | | | | | | | | |
| mean | — | — | 21.7 | — | 23.3 | — | 24.0 | — | 24.0 | 2 |
| range | 18.2 | — | 18.8-23.1 | 21.7 | 20.4-25.3 | 21.3 | 22.2-26.2 | — | 21.7-26.7 | 24.4 |

1: Data from Duellman, 1956.

## TABLE 1

*Phrynohyas* from Middle America

| . *spilomma*[1] | | *P. modesta*[1] | | Guatemala | | Honduras | | Costa Rica | | Panama | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ |
| 9 | 85 | 13 | 14 | 53 | 20 | 1 | 4 | 2 | 9 | 4 | 1 |
| .7<br>87.0 | 67.7<br>56.0-86.5 | 63.7<br>54.0-69.5 | 63.5<br>52.0-80.5 | 63.6<br>54.5-71.1 | 64.6<br>60.5-79.3 | —<br>67.0 | 66.2<br>62.7-68.5 | 81.5<br>74.3-88.6 | 77.5<br>54.5-94.1 | 88.9<br>84.0-92.0 | —<br>82.0 |
| .8<br>40.0 | 32.6<br>27.0-41.0 | 31.0<br>25.5-33.5 | 31.7<br>26.0-40.0 | 30.2<br>28.0-34.2 | 31.1<br>28.8-36.4 | —<br>31.3 | 32.9<br>30.9-34.0 | 38.1<br>34.4-41.7 | 37.2<br>29.6-45.8 | 41.8<br>40.6-43.5 | —<br>39.4 |
| .9<br>35.0 | 27.8<br>22.5-34.5 | 25.5<br>20.5-29.0 | 26.5<br>21.5-32.5 | 24.8<br>22.5-30.2 | 25.8<br>23.5-30.8 | —<br>26.5 | 27.3<br>24.5-28.4 | 32.6<br>29.6-35.5 | 31.7<br>26.0-35.7 | 35.9<br>32.5-38.3 | —<br>34.5 |
| .7<br>26.0 | 20.7<br>16.5-27.0 | 19.5<br>16.5-22.5 | 19.5<br>17.0-23.0 | 19.2<br>17.3-21.9 | 19.8<br>18.8-21.7 | —<br>20.8 | 20.0<br>19.1-20.9 | 24.0<br>22.4-25.5 | 23.8<br>18.9-27.7 | 25.2<br>23.5-26.0 | —<br>23.8 |
| .2<br>27.0 | 22.3<br>19.0-27.0 | 20.8<br>17.5-23.0 | 20.9<br>18.0-26.0 | 19.3<br>17.5-21.4 | 20.2<br>18.5-22.8 | —<br>20.8 | 20.7<br>20.1-21.4 | 25.1<br>22.5-27.7 | 25.4<br>19.8-30.0 | 27.0<br>25.0-28.6 | —<br>25.3 |
| .1<br>8.0 | 6.1<br>5.0-7.5 | 5.6<br>4.5-6.5 | 5.8<br>5.0-7.0 | 5.6<br>4.5-6.6 | 6.2<br>5.4-7.8 | —<br>5.5 | 6.1<br>5.9-6.6 | 6.5<br>6.0-7.0 | 6.3<br>4.0-7.0 | 8.1<br>7.5-9.2 | —<br>7.5 |
| .9<br>6.5 | 4.9<br>3.5-6.0 | 4.7<br>4.0-5.0 | 4.8<br>4.0-5.0 | 4.8<br>4.2-5.8 | 5.1<br>4.5-5.8 | —<br>4.7 | 4.8<br>4.7-5.1 | 6.0<br>6.0-6.0 | 5.5<br>4.5-6.5 | 6.6<br>6.5-7.0 | —<br>5.9 |
| .8<br>51.6 | 47.7<br>42.9-52.5 | 48.7<br>46.8-51.2 | 49.9<br>46.8-55.9 | 48.5<br>43.9-53.0 | 48.2<br>45.9-50.4 | —<br>46.7 | 49.7<br>49.3-50.3 | 46.7<br>46.3-47.1 | 48.2<br>45.2-52.1 | 47.0<br>45.1-48.9 | —<br>48.0 |
| .1<br>33.3 | 30.4<br>27.0-33.1 | 30.6<br>28.8-32.6 | 30.8<br>28.6-32.8 | 29.8<br>27.7-32.8 | 30.8<br>26.0-32.7 | —<br>31.0 | 30.2<br>29.2-32.0 | 29.5<br>28.8-30.1 | 31.3<br>26.9-43.1 | 28.3<br>27.6-29.0 | —<br>29.0 |
| .4<br>36.4 | 32.6<br>29.2-36.0 | 32.6<br>31.4-34.3 | 32.9<br>31.2-35.1 | 30.0<br>27.0-33.8 | 31.3<br>28.8-32.4 | —<br>31.0 | 31.3<br>29.5-32.8 | 30.8<br>30.4-31.3 | 33.5<br>29.4-50.8 | 30.4<br>29.5-31.9 | —<br>30.8 |
| .5<br>33.3 | 27.3<br>22.2-34.3 | 27.1<br>25.6-30.6 | 28.0<br>25.5-32.4 | 28.7<br>24.2-34.1 | 30.3<br>25.9-35.1 | —<br>26.4 | 29.6<br>28.0-32.7 | 26.0<br>25.3-26.7 | 25.4<br>14.4-29.8 | 30.0<br>26.2-34.6 | —<br>29.6 |
| .0<br>26.1 | 21.9<br>18.2-26.3 | 22.8<br>19.2-23.9 | 22.9<br>19.0-26.5 | 25.0<br>22.2-28.1 | 25.1<br>22.9-27.1 | —<br>22.6 | 23.4<br>22.3-25.2 | 24.2<br>21.7-26.7 | 22.1<br>16.2-25.3 | 24.6<br>22.7-26.0 | —<br>23.3 |

TABLE 1

TABLE 1

## Measurements and Proportions of *Phrynohyas* from Middle America

| | *P. latifasciata*[1] | | Sinaloa | | Nayarit | | Colima-Guerrero | | Oaxaca-Veracruz | | *P. spilomma*[1] | | *P. modesta*[1] | | Guatemala | | Honduras | | Costa Rica | | Panama | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ |
| Number of Specimens | 1 | 0 | 6 | 1 | 17 | 1 | 5 | 0 | 4 | 3 | 109 | 85 | 13 | 14 | 53 | 20 | 1 | 4 | 2 | 9 | 4 | 1 |
| Body Length mm | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 80.9 | — | 84.9 | — | 80.3 | — | 65.6 | 54.7 | 68.7 | 67.7 | 63.7 | 63.5 | 63.6 | 64.6 | — | 66.2 | 81.5 | 77.5 | 88.9 | — |
| range | 68.0 | | 74.2-90.2 | 89.0 | 81.1-92.6 | 95.8 | 63.5-92.0 | — | 55.9-69.0 | 47.4-60.9 | 48.0-87.0 | 56.0-86.5 | 54.0-69.5 | 52.0-80.5 | 54.5-71.1 | 60.5-79.3 | 67.0 | 62.7-68.5 | 74.3-88.6 | 54.5-94.1 | 84.0-92.0 | 82.0 |
| Tibia Length mm | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 35.7 | — | 39.7 | — | 34.5 | — | 30.3 | 27.2 | 32.8 | 32.6 | 31.0 | 31.7 | 30.2 | 31.1 | — | 32.9 | 38.1 | 37.2 | 41.8 | — |
| range | 30.0 | — | 33.5-39.3 | 39.5 | 37.9-42.8 | 42.9 | 32.0-42.0 | — | 26.0-33.0 | 24.1-30.1 | 22.5-40.0 | 27.0-41.0 | 25.5-33.5 | 26.0-40.0 | 28.0-34.2 | 28.8-36.4 | 31.3 | 30.9-34.0 | 34.4-41.7 | 29.6-45.8 | 40.6-43.5 | 39.4 |
| Foot Length mm | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 32.1 | — | 35.0 | — | 29.7 | — | 24.4 | 22.4 | 27.9 | 27.8 | 25.5 | 26.5 | 24.8 | 25.8 | — | 27.3 | 32.6 | 31.7 | 35.9 | — |
| range | 28.5 | — | 30.0-35.1 | 35.5 | 31.0-37.1 | 40.1 | 26.0-32.0 | — | 21.2-26.0 | 19.4-25.9 | 19.0-35.0 | 22.5-34.5 | 20.5-29.0 | 21.5-32.5 | 22.5-30.2 | 23.5-30.8 | 26.5 | 24.5-28.4 | 29.6-35.5 | 26.0-35.7 | 32.5-38.3 | 34.5 |
| Head Length mm | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 23.8 | — | 25.0 | — | 23.6 | — | 19.5 | 17.4 | 20.7 | 20.7 | 19.5 | 19.5 | 19.2 | 19.8 | — | 20.0 | 24.0 | 23.8 | 25.2 | — |
| range | 20.5 | — | 22.5-26.2 | 25.7 | 23.0-26.6 | 28.1 | 20.0-27.0 | — | 15.8-21.0 | 15.4-18.9 | 16.0-26.0 | 16.5-27.0 | 16.5-22.5 | 17.0-23.0 | 17.3-21.9 | 18.8-21.7 | 20.8 | 19.1-20.9 | 22.4-25.5 | 18.9-27.7 | 23.5-26.0 | 23.8 |
| Head Width mm | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 25.8 | — | 27.0 | — | 26.0 | — | 20.5 | 18.1 | 22.2 | 22.3 | 20.8 | 20.9 | 19.3 | 20.2 | — | 20.7 | 25.1 | 25.4 | 27.0 | — |
| range | 22.0 | — | 24.0-27.8 | 28.5 | 26.0-28.2 | 30.5 | 21.0-29.0 | — | 16.5-23.0 | 15.8-20.1 | 16.0-27.0 | 19.0-27.0 | 17.5-23.0 | 18.0-26.0 | 17.5-21.4 | 18.5-22.8 | 20.8 | 20.1-21.4 | 22.5-27.7 | 19.8-30.0 | 25.0-28.6 | 25.3 |
| Interorbital Distance mm | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 7.5 | — | 7.8 | — | 7.5 | — | 5.7 | 5.5 | 6.1 | 6.1 | 5.6 | 5.8 | 5.6 | 6.2 | — | 6.1 | 6.5 | 6.3 | 8.1 | — |
| range | 6.0 | — | 6.9-8.2 | 9.5 | 7.0-9.4 | 8.8 | 5.5-9.0 | — | 4.6-7.0 | 5.1-5.8 | 4.0-8.0 | 5.0-7.5 | 4.5-6.5 | 5.0-7.0 | 4.5-6.6 | 5.4-7.8 | 5.5 | 5.9-6.6 | 6.0-7.0 | 4.0-7.0 | 7.5-9.2 | 7.5 |
| Internarial Distance mm | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 5.6 | — | 6.2 | — | 6.2 | — | 4.9 | 4.4 | 4.9 | 4.9 | 4.7 | 4.8 | 4.8 | 5.1 | — | 4.8 | 6.0 | 5.5 | 6.6 | — |
| range | 4.0 | — | 4.9-6.1 | 6.2 | 5.5-6.7 | 6.5 | 5.5-7.0 | — | 4.1-6.0 | 3.9-4.8 | 3.5-6.5 | 3.5-6.0 | 4.0-5.0 | 4.0-5.0 | 4.2-5.8 | 4.5-5.8 | 4.7 | 4.7-5.1 | 6.0-6.0 | 4.5-6.5 | 6.5-7.0 | 5.9 |
| % Tibia Length/Body Length | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 44.2 | — | 46.8 | — | 47.6 | — | 46.2 | 49.8 | 47.8 | 47.7 | 48.7 | 49.9 | 48.5 | 48.2 | — | 49.7 | 46.7 | 48.2 | 47.0 | — |
| range | 44.1 | — | 42.5-45.6 | 44.4 | 44.6-48.4 | 44.8 | 45.6-50.7 | — | 44.1-47.8 | 49.1-50.3 | 44.1-51.6 | 42.9-52.5 | 46.8-51.2 | 46.8-55.9 | 43.9-53.0 | 45.9-50.4 | 46.7 | 49.3-50.3 | 46.3-47.1 | 45.2-52.1 | 45.1-48.9 | 48.0 |
| % Head Length/Body Length | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 29.5 | — | 29.4 | — | 32.5 | — | 29.6 | 33.0 | 30.1 | 30.4 | 30.6 | 30.8 | 29.8 | 30.8 | — | 30.2 | 29.5 | 31.3 | 28.3 | — |
| range | 30.1 | — | 27.6-31.5 | 28.8 | 28.0-31.3 | 29.3 | 31.5-33.3 | — | 28.3-30.4 | 32.8-33.3 | 27.9-33.3 | 27.0-33.1 | 28.8-32.6 | 28.6-32.8 | 27.7-32.8 | 26.0-32.7 | 31.0 | 29.2-32.0 | 28.8-30.1 | 26.9-43.1 | 27.6-29.0 | 29.0 |
| % Head Width/Body Length | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 32.0 | — | 31.8 | — | 29.6 | — | 31.1 | 31.9 | 32.4 | 32.6 | 32.6 | 32.9 | 30.0 | 31.3 | — | 31.3 | 30.8 | 33.5 | 30.4 | — |
| range | 32.3 | — | 30.3-33.5 | 32.0 | 29.4-35.0 | 31.8 | 27.7-31.5 | — | 29.2-33.3 | 31.0-32.3 | 29.1-36.4 | 29.2-36.0 | 31.4-34.3 | 31.2-35.1 | 27.0-33.8 | 28.8-32.4 | 31.0 | 29.5-32.8 | 30.4-31.3 | 29.4-50.8 | 29.5-31.9 | 30.8 |
| % Interorbital Distance/ Head Width | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 29.0 | — | 28.9 | — | 28.7 | — | 28.0 | 30.5 | 27.5 | 27.3 | 27.1 | 28.0 | 28.7 | 30.3 | — | 29.6 | 26.0 | 25.4 | 30.0 | — |
| range | 27.3 | — | 27.0-31.2 | 33.3 | 25.8-33.3 | 28.8 | 26.2-31.0 | — | 26.1-31.1 | 28.3-32.3 | 23.8-33.3 | 22.2-34.3 | 25.6-30.6 | 25.5-32.4 | 24.2-34.1 | 25.9-35.1 | 26.4 | 28.0-32.7 | 25.3-26.7 | 14.4-29.8 | 26.2-34.6 | 29.6 |
| % Internarial Distance/ Head Width | | | | | | | | | | | | | | | | | | | | | | |
| mean | — | — | 21.7 | — | 23.3 | — | 24.0 | — | 24.0 | 24.5 | 22.0 | 21.9 | 22.8 | 22.9 | 25.0 | 25.1 | — | 23.4 | 24.2 | 22.1 | 24.6 | — |
| range | 18.2 | — | 18.8-23.1 | 21.7 | 20.4-25.3 | 21.3 | 22.2-26.2 | — | 21.7-26.7 | 24.4-24.7 | 19.1-26.1 | 18.2-26.3 | 19.2-23.9 | 19.0-26.5 | 22.2-28.1 | 22.9-27.1 | 22.6 | 22.3-25.2 | 21.7-26.7 | 16.2-25.3 | 22.7-26.0 | 23.3 |

1: Data from Duellman, 1956

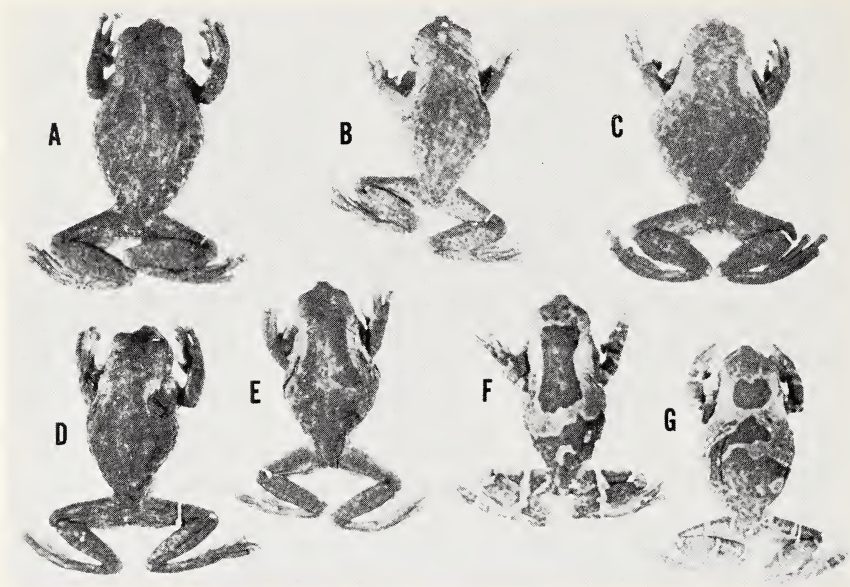


*Figure 1.* Series of *Phrynohyas venulosa* collected 9.4 miles south of Escuinapa, Sinaloa, Mexico. These frogs exhibit both unicolor and blotched color patterns.

and Nayarit, also suggests that the specimen is a young male. If the Sinaloan specimens referred to *P. latifasciata* represent a population distinct from *P. inflata*, then differences in proportions might be anticipated. It is apparent from Table 1 that the additional material from southern Sinaloa and Nayarit is intermediate between *P. latifasciata* and *P. inflata* in measurable characters. Although only two adult females of *Phrynohyas* are known from western Mexico, data suggest that females attain a larger size than males.

The development of the dorsal pustules in the *Phrynohyas* from Sinaloa and Nayarit varies considerably. The series includes animals with a nearly smooth dorsum, animals with moderately developed pustules, and animals with well developed pustules. The range of variation in this character encompasses the differences attributed to *latifasciata* and *inflata*. A specimen from Nayarit (CSCLB 641) that was preserved in alcohol has a relatively smooth skin. Additional specimens (CSCLB 625-640) collected from the same locality and on the same night were fixed in ten percent formalin and then preserved in alcohol. These specimens exhibit a wide range of variation in skin texture but in all cases are more rugose than the specimen initially preserved in alcohol. This suggests that the type of *latifasciata* was fixed in alcohol, apparently a common practice in the late 1800s.

The differences in coloration and pattern between species of *Phrynohyas*, as pointed out by Duellman (1956), include the nature of the dorsal color

pattern and the arrangement and size of the transverse leg bands. These differences also form the primary basis for the key to the adult *Phrynohyas* (Duellman, 1956:43-44). A series of seven specimens from Sinaloa (LACM 6314-19, 7245) exhibits a range of variation in dorsal color pattern encompassing three of the nominal species of *Phrynohyas* from Mexico (Fig. 1). Five of the specimens have a pattern similar to the unicolor form of *P. spilomma*, originally considered distinct and referred to *P. modesta* by Duellman (1956). Dorsally these specimens are mottled brown on tan, or dark brown on brown. Two of the specimens (D and E) show a slight indication of a darker mid-dorsal color, a condition considered intermediate between the unicolor phase and the blotched forms (F and G). The upper surface of the thighs is unicolor or speckled dark brown (A through E). Duellman (1956:27) pointed out that the unicolor brown dorsum and the speckled condition of the hind legs is typical of specimens of *P. modesta* found in southern Mexico and Guatemala. A second dorsal color pattern (F) consists of a light brown ground color with a large chocolate brown patch extending posteriorly from behind the eyes to near mid-body. A broad band of ground color bounds a posterior brown patch that continues to the vent and onto the dorsal surface of the thighs. The brown bands on the legs are separated by tan interspaces. This color pattern is typical of the specimens from Colima and Guerrero referred to *P. inflata* and shows striking similarities to the specimen from Michoacán figured by Duellman (1956:pl. II, fig. 1). Specimen G has a dorsal color pattern similar to specimen F but differing in having the anterior dorsal patch olive brown and broken into two parts rather than forming a continuous central patch. The middle spot is connected by a narrow band to the posterior blotch. The presence of two or more anterior dorsal spots is characteristic of the nominal species *Phrynohyas latifasciata* (Duellman, 1956:25, pl. III, fig. 1). The bands on the legs are not as wide as in the type of *latifasciata* (three times the width of the interspaces) but rather are very much like the condition of specimen F and the type of *P. inflata*. The vocal sacs of the Sinaloan frogs in life varied from chocolate brown to dark olive. With the differences in coloration of the vocal sacs noted in the Sinaloan series, it is not surprising to find that Boulenger (1882:327-328) described the type of *P. latifasciata* as possessing black vocal bladders. In life, the ventral surfaces of the *Phrynohyas* from Sinaloa vary from a dirty white to brownish white. The throat is usually creamy white with or without brown vermiculations.

In the series of specimens from Nayarit (Fig. 2), the anteriodorsal blotch is generally continuous in most specimens. However, one individual (A) has the anterior blotch broken into two parts. The nature of this break in the blotch is easily traced to the solid blotched pattern through intermediate specimens (B, C, G). In addition to the split of the anterior central patch, there is considerable variation in other specimens in the shape of the blotch. Certain individuals have a rectangular shaped blotch (E, H); some exhibit an

hourglass-shaped blotch (J, N). Some have posterior indentations of the blotch (K, L), anterior indentations of the blotch (B, G), or both (C, I, M). The color of the blotch varies from a uniform chocolate (E) to a mottled light brown blotch that is darker laterally (N). Some individuals have isolated circles of ground color within the blotch (F, G). In two specimens (M and N) the anterior and posterior blotches connect, while in others (L and O) the two dorsal blotches are almost completely fused.

In addition to the variation in dorsal pattern, the Nayarit series (Fig. 2) also exhibits a wide range of variation in color pattern of the legs. Some specimens have continuous bands on the femur and tibia of both hind legs (A, E, N). In some the bands are four times the interspace width (J, O); in some they are only twice the interspace width (B, C). There are progressive stages from specimens with nearly unicolor legs (L) through an individual with one tibia solid and one banded (H), or both tibiae solid (F, G), to specimens on which the interspaces do not meet across the face of the tibia on

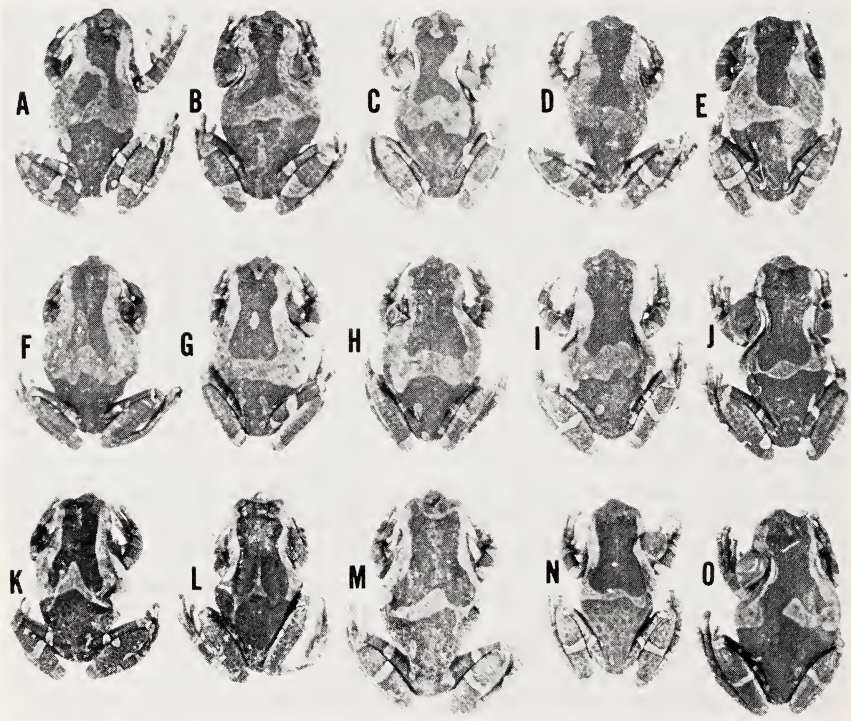


*Figure 2.* Selected individuals from a series of *Phrynohyas venulosa* collected 0.1 mile west of the junction of Mexico Highway 15 and Highway 46 (=22.9 miles east of San Blas), Nayarit, Mexico. The specimens show variation in dorsal color pattern and leg pattern.

either one side (K) or both sides (J). The leg markings vary from nearly unicolor (D, O) to a banded condition with varying degrees of spotting or marbling with a darker color (I, K). Most, but not all, of the leg bands are edged in dark brown. The Nayarit specimens possess a brownish white to creamy white venter, generally with some brown marking on the chin. The vocal sacs vary from light brown and olive to dark brown.

I examined the six specimens previously called *P. inflata* from western Mexico and found no differences between these specimens and the Nayarit or Sinaloa material, either in measurements or in proportions (Table 1). In terms of coloration and pattern, the six known specimens of *P. inflata* are almost exactly duplicated in the series from Nayarit. A single specimen (KU 73879) taken approximately halfway between the localities of the Nayarit and Sinaloan series possesses characteristics typical of some of the Nayarit specimens as well as of one of the Sinaloan specimens.

The description and illustration of *P. corasterias* (Shannon and Humphrey, 1957:15-18) indicate that this nominal species shares characters of color and pattern with some of the Nayarit material. In addition, the condition of the subarticular tubercle on the penultimate joint of the fourth finger (toe) varies from a bifid condition to a typical round condition in both the Nayarit and Sinaloan material. The webbing characters appear to be constant in all specimens examined from western Mexico and, in general, are the same as the illustration of the hand and foot of *P. corasterias* (Shannon and Humphrey, 1957:17, fig. 2). The other characters supposedly diagnostic of *P. corasterias* are well within the range of variation found in the Nayarit and Sinaloan series. Duellman (1961:45-46) considered the holotype of *P. corasterias* as a representative from the population of frogs from Colima, Michoacán, and Guerrero. The new material from Sinaloa and Nayarit indicates that there is extensive overlap between the characters used to distinguish between *P. latifasciata* and *P. inflata* and argues for recognition of but a single species of *Phrynohyas* in western Mexico.

*Southern Mexico-Northern Central America.*—The *Phrynohyas* from southern and eastern Mexico and northern Central America were considered by many workers to represent two species, *P. spilomma* and *P. modesta* (Smith and Taylor, 1948; Duellman, 1956, 1960; Neill and Allen, 1959a, 1959b; Neill, 1965; Stuart, 1963). Recently, Duellman (1966:277) presented evidence to show that *P. modesta* was a color variant of *P. spilomma*. Examination of material from Mexico, Guatemala, and Honduras augments the conspecificity of *P. modesta* and *P. spilomma*.

In his monograph of the genus in 1956, Duellman examined 335 specimens of *P. spilomma*. I have examined an additional 85 specimens. The measurements and ratios for the adult specimens are listed in Table 1. It is immediately obvious from the measurements that presumed *P. spilomma* generally average smaller than specimens of *Phrynohyas* from western Mexico.

*Figure 3.* Part of a large series of *Phrynohyas venulosa* from Cuyuta, Guatemala. These specimens show a gradation from unicolor to blotched dorsal pattern.

However, it should be pointed out that there is overlap in the ranges of all measurements of the frogs from southern and eastern Mexico and west Mexican *Phrynohyas*. In addition, the averages of the ratios are nearly the same from Sinaloa, Mexico to Honduras. While there is considerable variation in the measurements and proportions of this sample, there is no consistent geographic variation within the sample. Besides the overlap in measurements and proportions, there is a wide range of variation in skin texture. No consistent differences in skin texture or glandular development exist to aid in distinguishing the west Mexican individuals from those referred to *P. spilomma*.

The primary characters, other than overall size, that have been used to distinguish between eastern Mexican and Central American *Phrynohyas* and the *Phrynohyas* from western Mexico are differences in coloration and pattern. Examination of a large series of *Phrynohyas* from Cuyuta, Guatemala (AMNH 74377-90, +58) indicates that all the pattern types characteristic of *Phrynohyas* from Mexico and northern Central America may be present in a single breeding population. Selected individuals in this series (Fig. 3) exhibit a gradation from unicolor to blotched pattern. Some possess a unicolor brown dorsum with various degrees of spotting on the back and legs (A and B);

some have faint traces of a dorsal pattern and leg barring (C and D); three individuals (E, F, and G) are heavily mottled dorsally, tending towards a uniform dorsal blotch similar to those frogs referred to *P. spilomma*, as figured by Duellman (1956:pl. IV, figs. 1 and 2); others (H, I, and J) exhibit various modifications of a dorsal pattern and barred legs; and two specimens (K and L) are nearly identical in pattern with specimens from Nayarit, Mexico (Fig. 2, D, F, N). Ventral coloration in these 12 specimens is uniform white or dirty white with some brown mottling on the throat, or white with numerous brown spots.

Others have mentioned the color patterns characteristic of populations in a single area (Neill, 1965:88). Honduranean specimens were described by Duellman (1956:32) as closely resembling those from La Libertád, Guatemala (Duellman, 1956:pl. IV, fig. 2) and considered typical of the nominal *P. spilomma*. Meyer (1966:173) reported five specimens from Honduras, all of which were unicolor. Thus in Honduras, as in Guatemala, British Honduras, and Mexico, *Phrynohyas* exhibits a wide range of color pattern within a single population or between populations.

*Costa Rica and Panamá.*—Material from lower Central America, although scanty, provides a basis for further understanding of the relationships between the populations of this wide ranging hylid frog. As previously mentioned, both unicolor and blotched forms are known from Honduras. The only

*Figure 4.* Costa Rican specimens of *Phrynohyas venulosa* showing the variation in coloration and size.

known specimen from Nicaragua has a blotched pattern typical of some of the Guatemalan individuals. All previously known specimens from Costa Rica and Panamá exhibited a blotched dorsal pattern and banded legs. These frogs were assigned to *Phrynohyas venulosa* by Taylor (1952:800) and Zweifel (1964:201), and to *Phrynohyas zonata* by Duellman (1956:37). Several additional specimens from Costa Rica closely resemble the individual illustrated by Duellman (1956:pl. V, fig. 2) from Palmar, Puntarenas Province, Costa Rica, and the individual illustrated by Zweifel (1964:206, fig. 5) from Nueva Gorgona, Panamá Province, Panamá. Thus it appeared that lower Middle American *Phrynohyas* were generally consistent in their color pattern and large size and possibly represented a species distinct from the *Phrynohyas* from Honduras and areas to the north.

In late May, 1964, four unicolor specimens of *Phrynohyas* were collected in the Atlantic drainage at Los Chiles, Alajuela Province, Costa Rica. These specimens are smaller than other Costa Rican individuals but larger than most specimens from Honduras and Guatemala. The measurements and proportions of all the specimens examined from Costa Rica and Panamá are listed in Table 1. The specimens from lower Central America are generally larger than individuals of *Phrynohyas* to the north, but, as was true with the forms already discussed, there is overlap with the northern Central American forms in most of the measurements and very little difference, if any, among the ratios.

Ten of the Costa Rican specimens that were examined are pictured (Fig. 4). The four Los Chiles specimens, three females and one male, range from dark brown to brownish tan dorsally (A through D). Three specimens have unicolor legs, while the fourth possesses many dark spots on the hind legs. Ventrally they are yellowish white with a faint brown mottling on the throat and belly. The dorsal pattern of the remaining six adults from Costa Rica consists of a wide dark brown blotch beginning between the eyes and extending along the lateral edge of the dorsal blotch to about mid-body. The width of the lateral band varies from a narrow line (E and F) to a wide band (I and J) and determines the shape of the dorsal blotch. The legs of all the specimens are variously crossed by solid bands or a series of broken bands which give the legs an overall mottled appearance. Ventrally, these frogs are yellowish white with a faint brown mottling on the throat or covered with numerous brown spots. The skin texture varies from nearly smooth (A, C, and I) to very rugose and pustulate (B, E, and G). The ventral surfaces also show some variation in pustulation.

The Panamanian specimens examined exhibit the pattern (Fig. 5) characteristic of most of the Costa Rican frogs. The dorsal blotches are somewhat narrower than in some of the Costa Rican individuals and the lateral bands from the eyes are correspondingly wider. Ventrally, these frogs show varying degrees of faint brown mottling.

The intermediate size of the Los Chiles specimens and the presence of

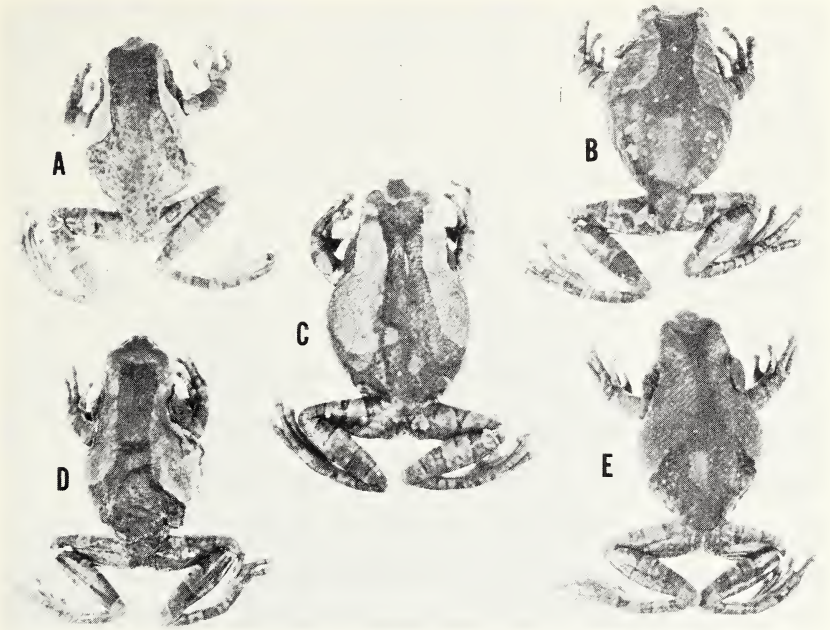


*Figure 5.* Panamanian specimens of *Phrynohyas venulosa* illustrating the lateral restriction of the dorsal blotch.

both color patterns in Costa Rica suggest that there is a very close relationship between the Panamanian and Costa Rican *Phrynohyas* and those to the north. Analyses of several characters of specimens from the entire range of the genus in Mexico and Central America indicate that there are no consistent differences among the populations studied. The characteristics utilized by Duellman (1956) to distinguish between species of *Phrynohyas* have been shown to exhibit considerable variation within each population and extensive overlap among several populations.

Based on the preceding discussion and analysis, I consider all known specimens of frogs of the genus *Phrynohyas* from Mexico and Central America as representative of a single, wide-ranging, variable species. All Middle American specimens presently referred to *Phrynohyas latifasciata, P. inflata, P. spilomma, P. modesta,* and *P. zonata* are regarded as representatives of *P. venulosa.*

Some comments concerning the South American species seem appropriate. Duellman discussed the relationship of *P. hebes* and *P. ingens. Phrynohyas hebes* is very close to *P. zonata* and Duellman (1956:42) suggested that they may be subspecifically related. *Phrynohyas ingens* differs from *P. venulosa* primarily in coloration and size, and Rivero (1961:131) considered *ingens* to

be a subspecies of *P. venulosa.* Based on a knowledge of the coloration and size variation found in the Middle American *Phrynohyas venulosa,* I suspect that detailed analysis of the South American forms will reveal that only a single, wide-ranging, and highly variable species may be involved.

## GROWTH AND ONTOGENETIC CHANGE

Zweifel (1964:201) described the eggs and larvae of *P. venulosa* from Panamá. He found that the larvae metamorphosed in the laboratory in approximately 37 days, and suggested that under natural conditions a faster rate of development might be expected. Several newly transformed frogs were collected in Costa Rica from June 18 to September 18, 1964. Two of these individuals (CRE 8178), measuring 26 and 27 mm in body length, were taken on the road about 12 miles NW of Liberia on the night of July 26. Field records indicate that three adult females (CRE 8102, 8105, 8121) were taken in the same area on the nights of June 29 and June 30. The retention of a few scattered eggs in the reproductive tracts of these frogs indicates that they had deposited their eggs shortly before being collected, probably the previous night. Both juveniles had attained the characteristic coloration typical of the adult frogs. If we assume that the females had finished depositing eggs just prior to their collection and that the young frogs began development at about that time, then the period from egg to frog encompassed thirty or more days. Zweifel (1964:205) pointed out that the characteristic adult pattern is not reached until several days after metamorphosis appears complete. The evidence, while circumstantial, suggests that under natural conditions the rate of development probably is faster than in the laboratory. In either case, the inferences concerning the length of time from egg laying to metamorphosis generally support Zweifel's findings. Other recently metamorphosed frogs from Parrita and Rincón de Osa, Costa Rica, are between 13 and 17 mm body length and do not exhibit the adult pattern. These specimens are assignable to *Phrynohyas venulosa* by their possession of green bones and the leg stripe characteristic of the recently transformed frogs (Zweifel, 1964:205).

Duellman (1956:33) mentioned the presence of ontogenetic change in the tibia/body length ratios of *Phrynohyas* from central Veracruz, Mexico. He stated that "Only in the small adults and juveniles does the tibia exceed 50 percent of the body length", and he refers to a graph of body length plotted against tibia length. All that can be determined from these data (Duellman, 1956:33, fig. 9) is that specimens above 60 mm body length generally have a shorter tibia and show a lower percent tibia/body length than do specimens below 60 mm. While there is no way to determine at what size (body length) he considered specimens to represent small adults and juveniles, it can be seen from his graph that there are specimens over 60 mm body length which have a tibia/body length ratio greater than 50 percent.

The tibia/body length ratios for 72 specimens from Guatemala show that ratios greater than 50 percent are found in six specimens ranging between 54.5 and 66.3 mm. The average body length for these six frogs is 60.7 mm, a value lower than the average for the total sample (Table 1). There are seven individuals with body lengths less than the average of 60.7 mm that have ratios lower than 50 percent. These seven specimens range between 58.7 and 60.5 mm ($\bar{x} = 59.7$ mm) and have tibia/body length percents ranging between 47.9 and 49.3 ($\bar{x} = 48.7$). It can be seen that there are about as many specimens with a tibia/body length ratio greater than 50 percent as there are with a tibia/body length ratio less than 50 percent at the same or larger body length. For the total sample this means that, proportionally, some of the smaller frogs have a slightly longer tibia than the larger frogs. These findings generally are supported by the few smaller individuals from other populations. In these instances the higher tibia/body length ratios are found in the smaller specimens. As Duellman and, to a degree, my data indicate, there is ontogenetic change in tibia length so that the smaller the individual, the relatively longer the tibia. The data presented by Duellman in support of this change are for animals greater than 40 mm in body length. Apparently, he did not have specimens smaller than 40 mm from central Veracruz, Mexico. A series of 20 specimens (TCWC 16782-91, 16800-09) from Zacapa, Santa Rosa Department, Guatemala, has body lengths between 24.4 and 30.1 mm ($\bar{x} = 26.3$ mm); the tibia length ranges between 11.5 and 14.1 mm ($\bar{x} = 12.6$ mm); and the percents of tibia/body length range between 44.6 and 51.5 ($\bar{x} = 47.9$). Unfortunately, no adults are available from this locality. A graph plotting body length against tibia length for these specimens (Fig. 6) exhibits the same distribution in reference to the 50 percent line as Duellman found for the adults from central Veracruz, Mexico. The majority of the specimens lie below the 50 percent line. These results indicate that a parabolic curve rather than a sigmoid curve of tibia/body length ratios would be found in a given population.

Two juvenile frogs (26 and 27 mm) and five adults (78.5 to 94.1 mm) from the same general locality in Costa Rica exhibit similar patterns. The smallest and the largest specimens have comparable ratios which are slightly lower than the intermediate sized specimens. Again the sample size, degree of differences among the ratios, and the lack of specimens from 30 to 70 mm body length do not allow for a meaningful analysis and only suggest the parabolic oscillation in ratios for a given population.

There is also an indication of ontogenetic change in the number of vomerine teeth. All juvenile frogs smaller than 30 mm body length that were examined averaged 4 to 5 fewer teeth than the adults from the same areas. Again the lack of sufficient material from the same population makes it difficult to evaluate these differences adequately.

Color pattern is the only other character which shows a well defined ontogenetic change. Recently metamorphosed frogs maintain the hind leg

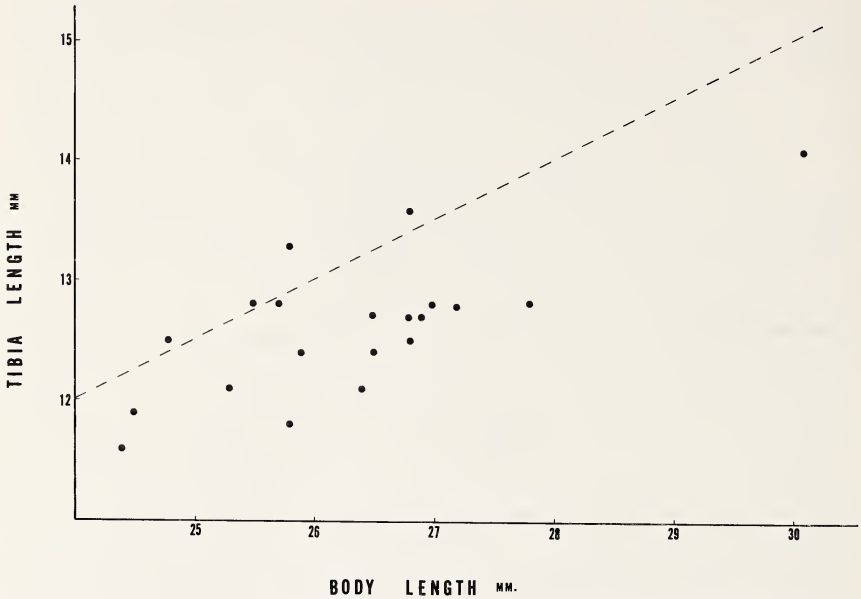


*Figure 6.* Graph plotting body length against tibia length for 20 small specimens of *Phrynohyas venulosa* from Zacapa, Guatemala. The 50 percent index is indicated by the dashed line.

stripe of the tadpoles for a few days after transformation. Zweifel (1964:205) described this characteristic coloration, and my material supports his findings. By the time the frogs reach 24 mm body length, they have attained the adult color pattern.

## Discussion

During the course of this study, several evolutionary trends among the different populations of *Phrynohyas* became obvious. I have already shown that color patterns, once thought to be consistent for each population, exhibit a wide range of variation from sample to sample or within a single population. The arrangement of the dorsal coloration in specimens from Mexico and Guatemala exhibits a clinal trend. All of the lower Middle American patterned specimens examined exhibit a single dorsal blotch. Most of the Guatemalan individuals possess a single dorsal blotch that extends from between the eyes to the vent. A single specimen from western Guatemala has the two blotched dorsal pattern characteristic of the western Mexican specimens. Individuals from Colima and Guerrero to the north exhibit a pattern of two blotches. In some specimens from the northern portion of the range of the genus along the

west coast of Mexico, the dorsal pattern consists of three blotches. The trend is towards a fragmentation of the dorsal blotch from northern Central America northward along the Pacific coast of Mexico.

In addition to the fragmentation of the dorsal pattern into two or three blotches, the anterior dorsal blotch tends to split along the longitudinal axis of the body. The split appears first in the Nayarit series and becomes prevalent in the southern Mexican and Guatemalan populations. There is no indication of a longitudinal split in dorsal patterns of specimens from Costa Rica and Panamá. The dorsal blotch is constricted in Panamanian and Costa Rican specimens, but most marked in the former. The lateral constriction narrows the dorsal blotch and decreases the amount of dark dorsal coloration, but in a different manner from the longitudinal splitting of the dorsal blotch found in the Guatemalan specimens.

The blotched dorsal coloration is considered the primitive condition. In the southern Mexican and Guatemalan populations, completely gradating series from blotched to unicolor forms are known. Apparently, the unicolor condition is a local variant, perhaps the result of a single gene mutation, which is distributed throughout the range of the species. The unicolor pattern may occur in all known specimens from a single locality, as is the case for the populations from near La Lima, Honduras, and Los Chiles, Costa Rica, or may appear with typical blotched forms without obvious intermediates, as in the population from near Escuinapa, Sinaloa.

Of primary importance to a discussion of the relationships among the major populations of *Phrynohyas* in Middle America is an understanding of the differences in sizes of the individuals from different populations. The data (Table 1) indicate that *Phrynohyas* from two areas are similar in size. The largest frogs are found in the terminal portions of the range of the species in Middle America, along the northwest coast of Mexico and in Costa Rica and Panamá. The central portion of the range is occupied by smaller frogs. In the past these differences have been interpreted as favoring the recognition of three species. As previously pointed out, there is complete overlap in the measurements from population to population and only slight differences between the ratios. Further, an examination of material from Central America clearly indicates a clinal gradation in body length for frogs from Guatemala (about 64.0 mm average size), Honduras (about 66.4 mm average size), Los Chiles, Costa Rica (about 70.5 mm average size), other Costa Rican specimens (about 83.0 mm average size), and Panamanian specimens (about 87.0 mm average size). This gradation generally is reflected in all other measurements as well (Table 1).

If a clinal trend in size does exist in western and southern Mexico, it is not immediately obvious for two reasons. First, there is insufficient material from Nayarit southward to Chiapas for adequate analysis. Secondly, the data for the southern and eastern Mexican populations, presented by Duellman (1956)

and included in Table 1, are lumped for all populations. It is obvious from these data that there is variation in size, sometimes marked and sometimes clinal, from population to population throughout the range of *Phrynohyas venulosa* in Middle America.

The larger specimens of *Phrynohyas* generally are found in areas of low mean annual rainfall, characterized by definite wet and dry seasons. The largest specimens were collected in western Mexico and along the Pacific coasts of Costa Rica and Panamá. Rainfall data from the major localities reveal that the largest individuals of the genus come from areas which have between 200 and 400 mm of precipitation in September and that the smaller individuals come from areas which have between 300 and 500 mm of precipitation in the same month (Vivo Escoto, 1964:200, fig. 11). Duellman (1956: 33) presented evidence which supports the proposed correlation between large size and drier environments. He recorded the largest specimens of his *Phrynohyas spilomma* from San Luis Potosí and Yucatan (mean monthly precipitation for September, between 100 and 300 mm). Frogs of intermediate size were taken from La Libertad, Guatemala (300 to 400 mm precipitation), while the smallest specimens are from Veracruz, Mexico (300 to 500 mm precipitation). This evidence indicates that there is a correlation between the size of the *Phrynohyas* and the amount of annual precipitation as evaluated by the mean monthly precipitation in September, the peak of the rainy season. Rainfall data for March (Vivo Escoto, 1964:202, fig. 12), the driest month of the year, also correlate with the sizes of the individuals from different populations. The largest specimens come from areas characterized by less than 25 mm precipitation in March, while the smallest specimens come from areas where the mean March precipitation exceeds 50 mm.

There are several selective forces that may operate to regulate an animal's size relative to the amount and distribution of the precipitation in a given habitat. The primary factor favoring large size in a dry habitat is water economy. The primary site of water loss in terrestrial and arboreal frogs is the skin. It has been well established that water loss via the skin is reduced in environments of high humidity and increased in environments of low humidity (Prosser and Brown, 1962:32). Thorson (1955:100-116) demonstrated that, within a species, small individuals lose water at a more rapid rate than large individuals. Schmidt-Nielsen (1964:23-32) discussed the advantage of a large body size in arid environments as an adaptation to cope with the continual problems of overheating and desiccation. Bogert and Cowles (1947:33) found that reptiles which live in moist environments lose moisture at a more rapid rate (in terms of the percentage of their original body weight) than those that are found in dry environments. They also point out that there is a definite correlation between habitat selection and ability to resist desiccation. Based on this evidence, it seems that the correlation between size and habitat in *Phrynohyas* represents an adaptive response to the environment. The occurrence of

the largest specimens in the driest areas suggests that the osmo-regulatory powers of *Phrynohyas* are increased in drier environments by large size.

There are other factors which should be considered in a discussion of the correlation between the frog's size and habitat. It is generally true that species reach their highest population density in areas of most favorable habitat. As a corollary, it may be assumed that the species probably is less successful in an unfavorable as opposed to a favorable habitat. Success in a less favorable habitat may involve some biological adaptation. In the long term this might lead to a gradual morphological modification through natural selection toward a closer adaptation to the specific habitat. An immediate measure advantageous to the species in an unfavorable habitat would be an increase in size. Salt (1962: 912) has pointed out that large size is a factor in certain avian species to increase their chance of success in unfavorable habitats as a temporary adaptation pending the eventual evolution of specific adaptations to the new habitat. Salt has shown that under some circumstances larger birds are more efficient than smaller individuals. For example, large birds can support a larger amount of tissue without a proportional increase in food requirement. If a large animal can feed at less energy output per gram than a small animal, then the large animal is more efficient, and greater efficiency has a selective value. A selective advantage could give the larger animal more latitude in moving into new habitats than the smaller animal. On this basis it is anticipated that the well adapted smaller form will occur in the favorable habitat, that is, the area occupied for the longest time. Conversely, the largest individuals are to be expected in unfavorable habitats, peripheral to the ecologic and distributional center of the species.

An examination of the distributions of the various *Phrynohyas* populations supports this suggestion. The most favorable habitat, as determined by species density based on collecting records, is in southeastern Mexico and northern Central America and is occupied by small individuals. That all the basic color patterns are represented in the populations from this area adds support to my contention that this area represents the possible center of dispersal of the species in Middle America. The Middle American center of dispersal for *Phrynohyas* is not necessarily the center of evolutionary origin for the species. I suggest that the general habitat now found in southeastern Mexico and northern Central America is similar to the habitat where *Phrynohyas* originated. In an historical sense, one would expect the best ecological fit between a species and its habitat to be in the area where adaptive evolution is most complete. In peripheral populations the degree of adaptation to the habitat is lower because there has been less time for evolutionary change.

An interesting sideline to this argument is that peripheral, drier environments, for several reasons, may not be able to support the same number of individuals as more mesic areas. This could explain the apparent greater density of smaller frogs in the more favorable humid habitats. If the populations of

larger frogs in dry regions are composed of fewer individuals than are the populations of smaller frogs, as is indicated by locality records, then another factor might favor a large size frog in drier areas. A large male potentially can call louder and attract more females from a wider area than can a small male at the same site. If the population density of *Phrynohyas* in dry environments is lower than in wet environments, then it would be advantageous to breeding males to be larger and have a louder call. Small males would not face the same problems in the more mesic environments where the population density is higher.

Bogert and Cowles (1947:33) found a rough correlation between the ability of representatives of a species to resist desiccation and the vagility of the species. The populations that exhibit wide latitudes in terms of physiological or ecological parameters usually have the greatest distribution and make the best colonizers. If it is assumed that the frog population that originally moved into peripheral habitats evolved a larger size to counteract suboptimal conditions in the new habitat, and that this larger size was also secondarily advantageous as a water conserving mechanism, then, after a given period of time, it might be expected that further adaptive modifications would appear. In the *Phrynohyas* from Costa Rica such an adaptation exists in the development of the dermal glands.

In specimens collected in late June and July, during the rainy season, the dermal glands in the neck region show relatively little development; the glands of specimens collected during the dry season, in February and March, show extensive development (Fig. 7). In many of the dry season specimens, glandular development is so extensive that parts of the tympanum are concealed (A). The tympanum is never concealed in Costa Rican specimens taken during the rainy season (B). Duellman (1956:31, 38) mentioned that many individuals of his *Phrynohyas spilomma* and *P. zonata* possess heavy glandular folds which obscure part or all of the tympanum. Because of the effects that the apparent

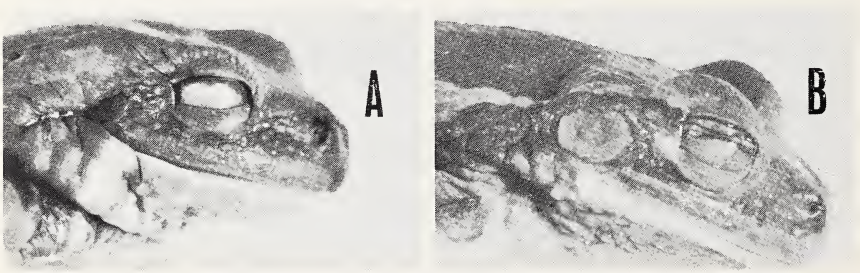


*Figure 7.* Lateral view of the heads of two Costa Rican *Phrynohyas venulosa* from Guanacaste Province showing the development of the dermal glands in the region of the tympanum. Specimen A was collected in February during the dry season; specimen B was collected in June during the rainy season.

seasonal variation in glandular development has on tympanum size, I did not consider tympanum size in the populational analysis. Small frogs have proportionally larger tympanums than larger frogs, and this difference is ontogenetic. Duellman (1956:39) mentioned a small form of his *Phrynohyas zonata* with a larger tympanum than in typical *P. zonata.*

The secretions of the dermal glands apparently are volatile and poisonous. The effectiveness of this secretion in deterring collectors (Smith, 1941:38; Duellman, 1956:41; Shannon and Humphrey, 1957:18; Neill and Allen, 1959: 26; Janzen, 1962:651) is well attested. It probably is very effective on natural predators, as well. Although differential predation on *Phrynohyas* in the dry season may account for the seasonal variation in glandular development, another explanation seems more plausible.

Slime secretion may be a factor decreasing skin permeability to water (Prosser and Brown, 1962:32). The use of slime secretion as a mechanism to prevent desiccation is well documented in lungfish (Herald, 1961:290; Smith, 1961:77-78). Vellard (1948:143) regarded the thick skin of the frog *Leptodactylus bufonius,* which is very rich in cutaneous glands, as protection against desiccation. McClanahan (1967:88) mentioned the appearance of dark, keratinized skin on *Scaphiopus* while the frog is hibernating, a change in integument effective in reducing water loss through the skin. Robert Stebbins (pers. comm.) reported the appearance of a cellophanelike membrane in *Pyxicephalus adspersus,* an African frog which is especially successful in arid environments. Stebbins wrote that whenever he wished to show the formation of this membrane, in which the frog completely encases itself, he merely placed the animal in a dry container for a few days. Neill and Allen (1959a:25) proposed that the slime of *Phrynohyas* might serve to prevent desiccation in addition to lessening predation. These authors point out that viscous organic liquids are comparatively resistant to evaporation. I have found that this secretion is water insoluble and is difficult to remove when dried. McConkey (*in* Duellman, 1956:41) mentioned that a collecting sac used to carry the frogs became stiff as a board a day or so after the secretion had dried. Vellard (1948:150) reports that in northern Argentina, these frogs use this cutaneous secretion to line the cavities of trees in which they seek refuge. If this is a response to aridity, then this peculiar behavior suggests that *Phrynohyas* has developed a modification to decrease water loss, which is similar to that mechanism utilized by lungfish.

All *Phrynohyas venulosa* examined have these glands, whether the frogs are from areas with a definite wet-dry season or from areas where there is some precipitation throughout the year. Frogs from the dry forests of Costa Rica, where there is a marked wet-dry season, apparently exhibit a change in the glandular development from season to season. It is suggested that the greater development and subsequent secretion of the glands in the dry season is produced as an adaptive response to arid environments. Additional investigation

with other populations of *Phrynohyas* is needed to corroborate the evidence. Similar adaptations may occur in other genera of frogs inhabiting arid environments.

## ACKNOWLEDGMENTS

I would like to express my appreciation to Jay M. Savage for his help and encouragement throughout the preparation of this report. Several other associates, especially Norman J. Scott, have offered suggestions or aided in the completion of this project in other ways. To them I extend my thanks. I am indebted to the following people and institutions for the loan of comparative material or for permission to examine specimens in their care: Richard J. Baldauf, Texas Cooperative Wildlife Collection (TCWC); James L. Christiansen, University of New Mexico (JLC); James R. Dixon, Los Angeles County Museum of Natural History (LACM); William E. Duellman, Museum of Natural History, University of Kansas (KU); Robert F. Inger and Hymen Marx, Field Museum of Natural History, Chicago (FMNH); Richard B. Loomis, California State College, Long Beach (CSCLB); Charles F. Walker, Museum of Zoology, University of Michigan (UMMZ); and Richard G. Zweifel, American Museum of Natural History (AMNH). Thanks are also due my wife, Mercedes, for checking the text and typing the manuscript, and to Robert J. Lavenberg and Richard A. Anderson for helping with the photographs. Part of the field work was done in 1962 with financial assistance from a Grant-in-Aid of Research from the Society of Sigma Xi. Specimens were collected in 1964 during the tenure of a National Science Foundation Summer Fellowship and in 1965 while participating in the program sponsored by the Organization for Tropical Studies.

## SPECIMENS EXAMINED

### MEXICO

Sinaloa: 9.4 mi S. Escuinapa (LACM 6314-19, 7245).
Nayarit: 46.5 mi S. Escuinapa (KU 73879); 22.9 mi E. San Blas (KU 74339, CSCLB 625-31, 633-41).
Colima: 1 mi N. Colima (UMMZ 80018); Paso del Río (UMMZ 108019).
Michoacán: Barranca de Bejuco (UMMZ 104814).
Guerrero: near La Venta (FMNH 10046, 10835, 10836).
Oaxaca: Temascal (LACM 28215-16, 36220-21).
Veracruz: 44 km S. Tampico (JLC 903-04); Salinas (TCWC 19103).

### GUATEMALA

Escuintla: Cuyuta (AMNH 74377-90 +58).
Santa Rosa: 45 km S. Guatemala City (LACM 8442); 23 km W. Zacapa (TCWC 16782-91, 16800-09).

HONDURAS

Cortés: 1 mi W. La Lima (TCWC 19180-84).

COSTA RICA

(Specimens designated CRE are in the University of Southern California collections.)
Alajuela: Los Chiles (CRE 7215 +1, 7219 +1).
Guanacaste: 20.6 mi N. Liberia (CRE 8157); 12.7 mi N. Liberia (CRE 8105, 8178 +1); 12.5 mi N. Liberia (CRE 8102); 12.4 mi N. Liberia (CRE 8121); 10.7 mi N. Liberia (CRE 8141); Río Higuerón, 0.5 mi E. Finca Jiménez (CRE 842); Finca Jiménez (CRE 892 +3).
Puntarenas: Parrita (CRE 6158 +2; 6159-60); Parrita, La Julieta (CRE 8253-54, 8258, 8264); 1⅞ mi S.W. Rincón de Osa (CRE 7237 +1); 5± mi W. Rincón de Osa (CRE 891).

PANAMA

Panamá: 3 mi S. Bejuco (AMNH 69803-04); Nueva Gorgona (AMNH 69805-06); 1 mi W. Nueva Gorgona (AMNH 69807).

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# NEW GENERA AND SPECIES OF WASPS OF THE TRIBE TRYPOXYLONINI FROM THE NEOTROPICAL REGION (HYMENOPTERA, SPHECIDAE, LARRINAE)

*By* A. S. MENKE

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# NEW GENERA AND SPECIES OF WASPS OF THE TRIBE TRYPOXYLONINI FROM THE NEOTROPICAL REGION (HYMENOPTERA, SPHECIDAE, LARRINAE)[1]

*By* A. S. Menke[2]

Abstract: *Pisoxylon xanthosoma*, new genus and new species, is described from Peru. Four subgenera are recognized in *Pison*: *Pison, Pisonoides, Krombeiniellum,* and the new subgenus *Entomopison* (type: *Pison pilosus* Smith, 1873). *Pison* (*Pison*) *eremnon* is described from Brazil. *Pison areolatus* Spinola, 1851, is transferred to the genus *Pisonopsis*. A lectotype is designated for *Pison variicornis* Reed, 1894, which is synonymized under *areolatus* Spinola. A key is provided to the genera of the Trypoxylonini and the subgenera of *Pison*. A checklist of the New World *Pison* is appended.

The following new generic and specific entities have been discovered while studying the tribe Trypoxylonini in connection with a world revision of the genera of the Sphecidae. This revision is being conducted by R. M. Bohart and the author. In addition to the new taxa described here, I have provided a key to the genera of the Trypoxylonini. Notes on the subgenera of *Pison,* a checklist of the New World *Pison,* and some new synonymy in *Pisonopsis* are also included.

The material on which this paper is based comes from several sources: the Los Angeles County Museum of Natural History; Department of Entomology, University of California, Davis; Carnegie Museum, Pittsburgh; and the U. S. National Museum, Washington, D. C. I would like to thank the curators of these institutions for the loan of this material. Deposition of types will be cited in the descriptions. Dr. I. H. H. Yarrow of the British Museum (Natural History) kindly sent me notes on the type of *Pison pilosum* Smith and related species.

## **Pisoxylon** new genus[3]

*Diagnosis*: Inner orbits deeply notched; antennal sockets not contiguous with frontoclypeal suture; flagellum with eleven articles; frontal carina narrowly forking above (Fig. 2); clypeus high, trapezoidal; mandible simple; labrum hidden, with two narrow apical fingerlike processes; mouthparts short, palpi 6-4; occipital carina meeting hypostomal carina near the latter's apex;

[1]Research supported by the National Science Foundation, grant numbers GB-5839 and GB-3074.

[2]Research Associate, Los Angeles County Museum of Natural History; Department of Entomology, University of California, Davis.

[3]Based on male, female unknown.

pronotal collar narrow; form of thorax as in *Trypoxylon,* landmark sulci of mesopleuron consisting of episternal sulcus curving forward ventrally but disappearing before meeting anterior margin, and a sulcus running from subalar pit to depression behind pronotal lobe; intercoxal carina straight (carina between mid - and hindcoxae); propodeum without carinae, propodeal enclosure not defined; area surrounding dorsal margin of propodeal orifice simple, not lamellate nor rimlike; no propodeal sternite; gaster sessile, compact (Fig. 5); wings as in *Trypoxylon*: one submarginal cell, marginal cell acuminate and with anterior veinlet of cell ($R_1$) extending a short distance beyond apex of cell, hamuli of hindwing divided into two groups, outermost group short and separated from basal group by much more than length of outer group; legs simple, mid - and hindcoxae contiguous, pulvilli moderately large, equal on all legs; gonostyle of male genitalia simple (Fig. 6).

*Type of genus*: *Pisoxylon xanthosoma* Menke.

*Distribution*: Known only from Peru in South America.

*Discussion*: This genus is very similar to *Trypoxylon,* but differs in having a nonpetiolate compact gaster (Fig. 5). *Trypoxylon* is a huge genus (over 350 species), and accordingly contains many divergent groups. Therefore it could be argued that *Pisoxylon* simply represents an extreme group within *Trypoxylon* and as such should be considered as a subgenus. However, despite the morphological complexity of *Trypoxylon,* it is still an easily recognized taxon because of the long clavate (and often petiolate) gaster. To place *Pisoxylon* in *Trypoxylon* would, in my opinion, tend to weaken a popular and morphologically sound generic concept.

## **Pisoxylon xanthosoma** new species

*Holotype male*: Length 9 mm.

*Color*: Straw yellow; frons, vertex and back of head black; antenna yellow basally but grading to black at tip; scutum black but with a large rectangular central yellow spot, and humeral area yellow; posterior half of scutellum black; metanotum with a small lateral black spot; dorsum of propodeum and median sulcus of posterior face black; subalar pit of mesopleuron black; metapleuron narrowly black beneath metapleural flange; gastral tergite I with a transverse subapical brownish band, remaining tergites slightly suffused with brown; tarsomere V of mid- and hindlegs and all pulvilli black; wings with a faint yellow tint, veins reddish brown.

*Vestiture*: Appressed hair of clypeus, lower frons and gena golden; rest of body with short, sparse, pale hair.

*Structure*: Flagellomeres IX and X shorter than preceding articles, flagellomere XI slightly longer than combined length of articles VIII-X, flagellomeres VI-VIII bearing narrow tyloides ventrally, flagellomere VIII swollen apicoventrally (Fig. 2); frontal carina Y-shaped, the stem bearing two short lateral arms just above antennal sockets (Fig. 2); frons minutely granulate

with moderate shallow punctation, dull; least interocular distance at vertex slightly greater than at clypeus (24.5:21.0); ratio of ocellocular distance to diameter of lateral ocellus to distance between lateral ocelli: 2.0:8.0:5.0; clypeal outline as in Figure 2; surface of scutum and scutellum less shiny than propodeum and pleura, punctation of thorax fine and sparse; propodeal dorsum finely diagonally ridged basally, ridges merging laterally with evanescent striatopunctation which rapidly becomes simple punctation; median sulcus of propodeal dorsum broad, and with fine transverse arcuate ridges; posterolateral corner of propleuron with a roughly egg-shaped platelike area covered with short hair and delimited inwardly by a carina; sternites VII-VIII as in Figures 3 and 4, respectively; genitalia as in Figure 6.

*Holotype male*: Pucallpa, Loreto, Peru, 200 m, April 10-19, 1965, J. Schunke. Type deposited in the Los Angeles County Museum of Natural History.

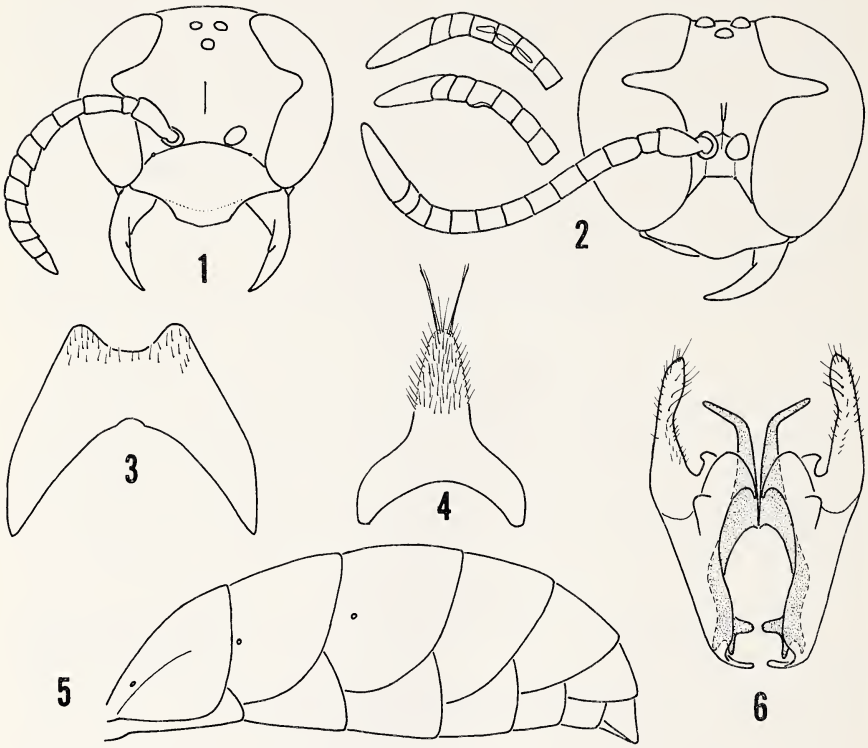
*Discussion*: The extensively yellow body of this wasp is distinctive, although a few Neotropical *Trypoxylon* species are similarly colored. The features of the head, especially the antenna, should separate *xanthosoma* from other species of *Pisoxylon* that may be discovered. The two narrow tufts of long setae at the apex of the last sternite are distinctive (Fig. 4). These setae project from the apex of the abdomen, giving the appearance of a sting.

## The subgenera of **Pison**

Three subgenera are currently recognized in *Pison*: *Pison, Pisonoides* and *Krombeiniellum*. *Krombeiniellum** is a valid subgenus in my opinion. It differs from typical *Pison* in having short dense hair on the eyes. Most *Krombeiniellum* have only two submarginal cells in the forewing, but there are several undescribed species from the Neotropical Region with three submarginals. The subgenus includes *browni* Ashmead, *differens* Turner, and *koreense* Radoszkowski. These three are Oriental species, but *koreense* has been successfully introduced to the United States (Krombein, 1958).

The taxon *Pisonoides* includes all other *Pison* species that have only two submarginals. However, like Turner (1916) and Leclercq (1965), I do not believe that *Pisonoides* is a valid subgenus if based solely on wing venation. The size of the second submarginal cell of *Pison* species having three submarginals varies from large to very small. In species in which the cell is pinhole size, some specimens exist in which the cell is entirely obliterated (*Pison xanthopum* Brullé, *inaequale* Turner and other African species, for example). The type species of *Pisonoides, Pison obliteratum* Smith, differs from most other *Pison* species in having a semipetiolate abdomen. This condition is found in at least two other two-celled *Pison* species: *icarioides* Turner and *difficile* Turner. It

*Richards (1962, p. 118) proposed *Krombeiniellum* for the preoccupied name *Paraceramius* Radoszkowski.




*Figures 1-6.* 1. Head of *Pison eremnon,* holotype. 2-6. *Pisoxylon xanthosoma,* holotype: 2. head, with three views of terminal flagellomeres, 3. sternite VII, 4. sternite VIII, 5. lateral view of gaster, 6. ventral view of genitalia (aedeagus is stippled).

would appear that if *Pisonoides* is to be recognized as a subgenus, it must be redefined on the basis of the semipetiolate abdomen and presence of two submarginal cells. All two-celled *Pison* with a nonsubpetiolate abdomen thus revert back to the typical subgenus *Pison*.

A fourth group of *Pison* species has been found which is sufficiently distinct to warrant subgeneric status. It is characterized as follows:

**Pison (Entomopison)** new subgenus

Mandible with a deep notch (or angle) on externoventral margin; forewing with three submarginal cells, the second petiolate; recurrent veins of forewing received by second submarginal, or first recurrent vein interstitial or received by first submarginal.

*Type of subgenus*: *Pison pilosum* Smith, 1873, present designation.

Except for the notched mandible, *Entomopison* is a typical *Pison* in every respect. Notched mandibles also occur in the trypoxylonine genus *Pisonopsis*, but this taxon differs from *Pison* in having oblique grooves on sternites III-IV, and a shorter marginal cell, the apex of which is rounded or truncate. Furthermore, in some species of *Pisonopsis* the female has a pygidium. *Pisonopsis* has a narrower (more transverse) clypeus than most *Pison* species. The clypeal outline of *Pison* usually approximates a high trapezoid.

*Entomopison* is a Neotropical group and from the material on hand, it is clear that there are at least ten species in South America, all of which are undescribed save for *pilosum, aurofaciale,* and *convexifrons*.

**Pison (Pison) eremnon** new species

*Holotype female*: length 14 mm; a large black, rather coarsely and irregularly punctate wasp.

*Color*: Black; inner face of hindtibia rust colored; anterior margin of forewing strongly infumate, hindwing faintly infumate anteriorly.

*Vestiture*: Appressed hair of face sparse, brown; head and thorax with long erect brown hair, propodeum posterolaterally with some shorter pale erect hair in addition to the brown hair; fine appressed hair of gastral tergites brown, tergites without transverse apical bands of hair.

*Structure*: Inner orbits converging above, ratio of interocular distance at clypeus and vertex: 49:34; lateral ocelli much closer to each other than to eyes, ratio of ocellocular distance to diameter of lateral ocellus to interocellar distance: 10:5.5:3; frons with a median longitudinal carina the length of which is equal to about two ocellus diameters; frons and clypeal disk closely to confluently punctured, punctures of two sizes, the larger ones scattered, interspaces weakly shagreened, surface subshining; clypeus with an obtusely trunctate median lobe which is broadly impunctate and shining; mandible with a small tooth on inner margin (Fig. 1); antenna as in Figure 1; collar weakly tumid mesally; scutum shagreened, dull, scutal punctures of two sizes, closely

punctate anteriorly, punctation becoming irregularly less dense posteriorly, where punctures are separated by one to one and a half puncture diameters; scutellar punctation sparser than that of scutum; metanotum with very fine, dense, pinhole punctures and a few scattered large punctures; propodeal dorsum with a median longitudinal ridge which is contained in a narrow sulcus, sulcus obscured by transverse striatopunctation basally, remainder of dorsum irregularly densely punctate, the punctures of uniform size, interspaces shining; punctures of propodeal side and posterior face of two sizes, smaller punctures dense, becoming weakly striatopunctate posterolaterally, larger punctures (about size of those on dorsum) sparse; upper two-thirds of vertical posterior face of propodeum with a deep sulcus; propodeum without lateral carinae; mesopleural punctation same as that of anterior one-half of scutum but interspaces shining; sulcus dividing metapleuron from propodeal side foveolate between upper and lower pits; metapleural flange narrowly lamellate; gastral segment I set off from remaining segments by a constriction, tergite I sharply transversely depressed subapically forming a bandlike margin; punctation of tergite I similar to that of posterior one-half of scutum, interspaces shining, punctation of II denser except for some polished subapical prominences, punctation of III-VI very dense and punctures of uniform size; sternites strongly shining, sparsely and finely punctate although with a few scattered larger punctures; marginal cell of forewing rounded apically, the apex just barely surpassing outer veinlet of third submarginal cell; first recurrent vein received by second submarginal cell, second recurrent interstitial.

*Holotype female*: Santarem, Brazil, H. H. Smith, deposited in the Carnegie Museum, Pittsburgh.

The large size, black body with dark hair, and rounded marginal cell quickly distinguish this wasp from all other known Neotropical *Pison*. The size of *eremnon* is exceeded only by the Old World species *regale* Smith and its relatives. The rounded marginal cell is a rarity in *Pison*, occurring only in a few Old World species.

## Checklist of New World **Pison**[4]
### subgenus **Pison**

*cameronii* Kohl, 1893. Mexico or Peru.
  *fasciatum* Kohl, 1883. (preocc.)
*chilense* Spinola, 1851. Chile.
*conforme* Smith, 1869. Mexico.
*cressoni* Rohwer, 1911. Nicaragua.
*eremnon* Menke, 1967. Brazil.

[4]*Pison argentinus* Schrottky, 1909; *P. flavopictus* Smith, 1860; *P. laetus* Smith, 1860; and *paraensis* Spinola, 1853 are no longer assignable to *Pison*. See Menke, 1968, for details.

*flavolimbatum* Turner, 1917. British Guiana.
?*laeve* Smith, 1856. "Georgia." Verification that this is a North American or a New World species is needed.
*maculipenne* Smith, 1860. Brazil.

subgenus **Krombeiniellum**

*koreense* Radoszkowski, 1887. Eastern United States, eastern Asia.

subgenus **Entomopison**

*aureofaciale* Strand, 1910. Paraguay.
*convexifrons* Taschenberg, 1870. Brazil.
*pilosum* Smith, 1873. Brazil.

New synonymy in **Pisonopsis**
**Pisonopsis areolatus** (Spinola)

*Pison areolatus* Spinola, 1851. *in* Gay, Historia Fisica y Politica de Chile, Zool., 6:327. Holotype ♀, Chile (type probably in Turin or Paris).

*Pison variicornis* Reed, 1894. Anal. Univ. Chile, 85:634. Lectotype ♂, Valparaiso, Chile (Museum of Comparative Zoology, Cambridge), present designation. New synonymy.

? *Pisonopsis anomala* Mantero, 1901. Bull. Soc. Ent. Ital., 33:202. Holo-♂ type , Rio Santa Cruz, Argentina (Museo Civico de Storia Naturale, Genoa). Tentative new synonymy.

This species has been assigned to *Pison* until now. I have studied material of a small black Chilean *Pisonopsis* which agrees perfectly with Spinola's description, and there is little doubt that the type of *areolatus* is this species. I have seen Reed's syntypes of *variicornis* and they agree with Spinola's description of *areolatus*. Mantero's description of *anomalus* seems to fit *areolatus*, but I have seen no Argentine material. *Pisonopsis areolatus* apparently is the only representative of the genus in Chile. Besides *areolatus* there is one other South American *Pisonopsis*: *australis* Fritz from Argentina. *Pisonopsis argentina* Schrottky is probably a species of a new genus belonging in the tribe Bothynostethini (see Menke, 1968).

Key to genera of the TRYPOXYLONINI

1. Forewing with one submarginal cell; antennal sockets not contiguous with frontoclypeal suture ..... 2
   Forewing with two or three submarginal cells; antennal sockets contiguous with frontoclypeal suture ..... 3

2. Gaster long, clavate, often petiolate, segment I usually slender, clublike, at least two times as long as wide; Old and New World ..... *Trypoxylon* Latreille

Gaster compact, sessile, segment I not elongate (Fig. 5); South America..... *Pisoxylon* Menke

3. Gaster compact, sessile, segment I not petiolate or at most subpetiolate in dorsal view; mesopleuron without coarse horizontal ridges; Old and New World ..... 4
   Gaster petiolate, segment I rodlike (tergite nodose at apex) and nearly as long as remaining segments combined; mesopleuron with many coarse horizontal ridges; Neotropical Region.....*Aulacophilus* Smith

4. Marginal cell of forewing rounded or truncate apically, the apex not or only slightly extending beyond outer veinlet of third submarginal cell, *and* externoventral margin of mandible notched or strongly angulate, *and* sternites III-IV with a lateral oblique groove; female gastral tergite VI usually flattened or with a distinct pygidium bounded by carinae; North and South America.....*Pisonopsis* Fox
   Marginal cell of forewing acute apically, the apex extending well beyond outer veinlet of third submarginal cell, or if apex rounded and/or not extending much beyond third submarginal (exceptional Old World species), then outer margin of mandible not notched; outer margin of mandible entire (except in some South American forms but wing characteristics typical); gastral sternites without oblique grooves; female gastral tergite VI conical, sometimes weakly keeled along midline; cosmopolitan .....*Pison* Jurine 5

5. Outer margin of mandible entire..... 6
   Outer margin of mandible notched or strongly angulate; South America.....subgenus *Entomopison* Menke

6. Eyes bare..... 7
   Eyes densely covered with short hair; Oriental Region, North and South America.....subgenus *Krombeiniellum* Richards

7. Gaster sessile, not subpetiolate, apical width of segment I much more than one-half apical width of II and usually subequal to II (dorsal view); forewing with two or three submarginal cells; Old and New World .....subgenus *Pison* Jurine
   Gaster subpetiolate, apical width of segment I about equal to one-half apical width of segment II; forewing with two submarginl cells; Australasian Region.....subgenus *Pisonoides* Smith

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# CONTRIBUTIONS IN SCIENCE

NUMBER 136 FEBRUARY 20, 1968

# A NEW PORCUPINE FROM THE MIDDLE PLEISTOCENE OF THE ANZA-BORREGO DESERT OF CALIFORNIA

## With notes on mastication in *Coendou* and *Erethizon*

*By* JOHN A. WHITE

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DOROTHY M. HALMOS
*Editor*

# A NEW PORCUPINE FROM THE MIDDLE PLEISTOCENE OF THE ANZA-BORREGO DESERT OF CALIFORNIA

## With notes on mastication in *Coendou* and *Erethizon*

*By* John A. White[1]

Abstract: A new species of *Coendou* is described from the Middle Pleistocene of the Anza-Borrego Desert.

The genera *Coendou* and *Erethizon* are distinguished from one another by means of inferred differences in mastication, and it is postulated that *Coendou* is ancestral to *Erethizon*.

### Introduction

A large and diversified collection of fossil vertebrates has been obtained from the highly fossiliferous badlands of the Vallecito Creek Valley and Fish Creek Wash areas of the Anza-Borrego Desert in the western Imperial Valley of Southern California. This collection has resulted from the extensive field operations in that area conducted by the Vertebrate Paleontology Section of the Los Angeles County Museum of Natural History under the direction of Theodore Downs.

The sediments comprise the Palm Springs formation (Woodring 1931; Dibblee 1954) and consist of mudstones, siltstones, and sandstones which are occasionally cross-bedded. That part of the formation from which the above collection was made is exposed on the south limb of a west-plunging anticline (Woodard 1963), and dips 24 to 26 degrees to the south. It is in continuous sequence through more than 10,000 feet. The porcupine specimens described herein have been collected from within the upper 3,000 feet of this section, which is Irvingtonian (Middle Pleistocene) in age (Downs 1957; White and Downs 1961; Howard 1963; White 1964).

### Acknowledgements

The author thanks the following individuals for permission to examine specimens in their care: Seth Benson, Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); W. A. Clemens and Theodore Eaton (Vertebrate Paleontology), and E. Raymond Hall and J. Knox Jones, Jr. (Mammalogy), Museum of Natural History, University of Kansas (KUM); C. L. Gazin and Clayton E. Ray (Vertebrate Paleontology), and David H. Johnson (Mammalogy), United States National Museum (USNM); Claude W. Hibbard, Museum of Paleontology, University of Michigan (UMM); J. R. Macdonald (Vertebrate Paleontology), and C. A. McLaughlin (Mammalogy), Los Angeles County Museum of Natural History (LACM); and

[1]Curator in Vertebrate Paleontology, The Museum, Idaho State University, and Research Associate, Los Angeles County Museum of Natural History.

Donald E. Savage, Museum of Paleontology, University of California, Berkeley.

For valuable suggestions the writer is indebted to the late R. A. Stirton, Claude W. Hibbard, and Theodore Downs. Theodore Downs and David E. Fortsch critically read the manuscript. John E. Mawby collected the type specimen. Kent Wilkinson made the stereo-photograph, and Lisa A. Hansen made the other illustrations.

The cooperation of the personnel and management of the Anza-Borrego Desert State Park is gratefully acknowledged.

The National Science Foundation supported this research through grants GB-1333 and GB-5116.

## SPECIMENS EXAMINED

An estimated 400 specimens of *Erethizon* and 25 *Coendou* were examined. Only the specimens that were measured are listed here with their museum numbers.

*Coendou mexicanus*: MVZ 116815, 116817, 124088; USNM (Mammalogy) 296308, 298915, 303135, 303277, 306980, 324110, 335666; skeletons: 240269, 240312, 257008, 257364; KUM (Mammalogy) 18190, 18191, 19888, 19889, 24489, 24490, 24491, 32180, 93790, 93791, 93793, 93794; UMM *Coendou* sp. V47106; ?*Coendou brachignathum* USNM (Vertebrate Paleontology) 13684.

*Erethizon dorsatum*: MVZ 4052, 4508, 4510, 4467, 4496, 51382, 40874, 42073, 42077, 42078, 42079, 46906, 53702, 53263, 58496, 67689, 68707, 68708, 74292, 79588, 84036, 84969, 84970, 87862, 89556, 106164; USNM (Mammalogy): skeletons: 49420, 90476, 192546, 241005; (Vertebrate Paleontology): 7668-7673, 7996, 8128, 8130, 8134, 8174.

A number of specimens of porcupines referable to the genus *Coendou,* to which belong the prehensile-tailed porcupines of the rain forests of Central and South America, have been collected in the above-mentioned geological section, and differ morphologically from known species of the genus to such a degree that they are assigned to a new species.

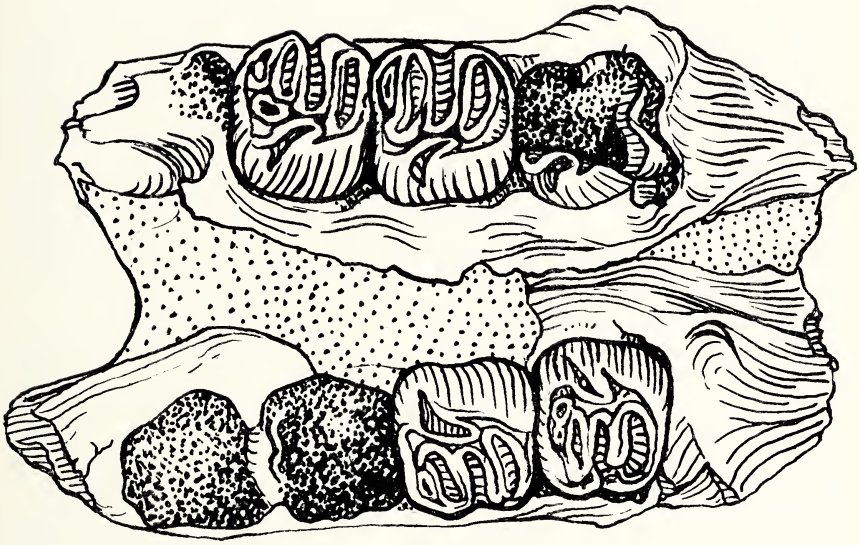
## **Coendou stirtoni** new species

*Type*: LACM 17633, fragmentary palate with $LP^4$- $M^1$, $RP^4$ (partial), $M^1$ and $M^2$ (Fig. 1).

*Type Locality*: LACM 1428, Arroyo Tapiado, Badlands in Anza-Borrego Desert State Park, San Diego County, California.

*Horizon*: Approximately 2900 feet stratigraphically below top of the Palm Spring formation in the Tapiado member of the formation (Woodard 1963).

Fig. 1A



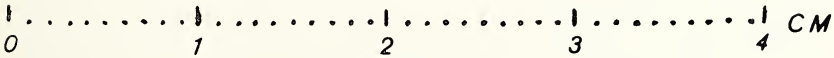



Fig. 1B

*Figure 1. Coendou stirtoni* n. sp., LACM 17633, type specimen, stereophotograph of the palate (A); ventral view of palate (B).

*Referred Specimens*: LACM 6136, a partial skeleton with palate and medial part of $RM^2$, ventral portion of rostrum, fragmentary left mandible with broken teeth, sacrum and 12 caudal vertebrae, proximal end of left radius, broken proximal right ulna, partial ischium with part of acetabulum, proximal end of left femur; 6210 and 6210A, two fragmentary left mandibles with broken teeth; 4325, a partial skeleton lacking skull parts, but with distal part of right humerus, right radius and ulna with distal epiphyses missing, proximal portion of left ulna, right femur with distal epiphysis missing, left astragalus, right calcaneus, left cuboideum, and seven phalangeal elements.

*Diagnosis*: Erethizontid with width of palate between right and left $P^4$'s at least 40 per cent of width of palate between $M^3$'s in adults; width of $P^4$ approximately the same as width of $M^1$; adults as large as a large adult *Erethizon*, and far larger than any species of living *Coendou*.

*Description*: The occlusal pattern of the cheek teeth in *Coendou stirtoni* is essentially the same as in other species of *Coendou* and in *Erethizon*. The large size of the teeth in the new species tends to cause the occlusal patterns of the cheek teeth to resemble those in *Erethizon* more than those in *Coendou*; however the living species of the latter genus have teeth that are markedly smaller in size than in *Erethizon* and in the larger, extinct species of *Coendou*. This marked difference in size may account for the dissimilarity of tooth pattern. $P^4$ is as wide as $M^1$ in the new species and in all specimens of living *Coendou* examined, while in all specimens of *Erethizon* $P^4$ is markedly larger than $M^1$. In juvenile specimens of *Erethizon*, $DM^4$ is as wide as $M^1$, and $DM^4$ and $P^4$ resemble one another morphologically in *Coendou* and *Erethizon*. In the type specimen of *C. stirtoni*, the broken roots of $DM^4$ are visible on the sides of the alveolus of $P^4$.

Although mandibular cheek teeth are unknown for *C. stirtoni*, $P_4$ in *Erethizon* is, on the whole, larger than $M_1$ while in *Coendou* the two teeth tend to be subequal in size. The relationship between $P^4$ and $M^1$ is more consistent than that between $P_4$ and $M_1$ (compare Figs. 4 and 5). The latter exhibits considerable variation and is of limited taxonomic use (Hibbard and Mooser 1963). Only in rare cases when $P_4$ is *markedly* larger than $M_1$ can *Erethizon* be identified by this character.

In mandibles LACM 6210A and 6136, the base of the ascending ramus indicates that it slanted posteriad, permitting the cheek teeth to be visible from the side (Hibbard and Mooser *ibid.*), as in other species of *Coendou*.

In mandibles LACM 6210 and 6210A the proximal, approximately three-fourths of the inflected angular process is present and is as in *Coendou*, wherein it is subparallel to a midline separating the mandibles, and not inflected to the degree it is in *Erethizon*. The greater inflection seems to reflect the marked divergence posteriad of the cheek teeth in the latter genus.

Unfortunately, only four skeletons each of *Coendou* and *Erethizon* were

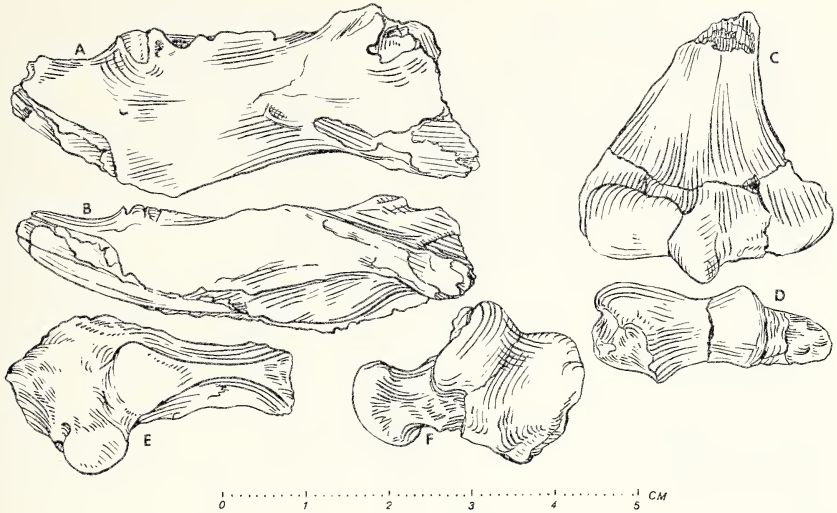



*Figure 2. Coendou stirtoni* n. sp. Lateral (A) and ventral (B) views of left mandible, LACM 6210A; anterior (C) and distal (D) views of right humerus; dorsal view of left astragalus (E), LACM 4325; and dorsal view of right calcaneus (F), LACM 4325.

available for comparison with two partial skeletons of *C. stirtoni. C. stirtoni* resembles both genera in most observable skeletal characters but differs in the following:

The medial epicondyle of the humerus (Fig. 2 C and D) in *Coendou* and in *C. stirtoni* is oriented laterad, whereas in *Erethizon* it extends posteriad. Since the digital flexor muscles have origin mostly on the medial epicondyle, one is tempted to relate this difference to the known difference in habitus existing between living *Coendou* and *Erethizon.* More needs to be known about the functional anatomy of these forms before such conclusions can be made, however.

The proximal articular surface of the radius in specimen LACM 6136 is ovoid, similar to the condition in *Coendou,* while in *Erethizon* it is rounded. The portion of the articular facet of the acetabulum present on the ischium in specimen LACM 6136 is elongated as it is in *Coendou,* while in *Erethizon* it is rounded. The femur (Fig. 3A) in specimens 6136 and 4325 has a well-developed third trochanter as in *Erethizon.* In *Coendou* this trochanter is poorly developed (Gupta 1966). The neck of the astragalus in specimen 4325 is distinct as in *Coendou* while in *Erethizon* it is less so.

The caudal vertebrae in specimen 6136 were not found in articular position, but when they are lined up in a sand box it seems likely they did articulate. The last caudal to have a zygapophyses is the ninth. If this interpretation is

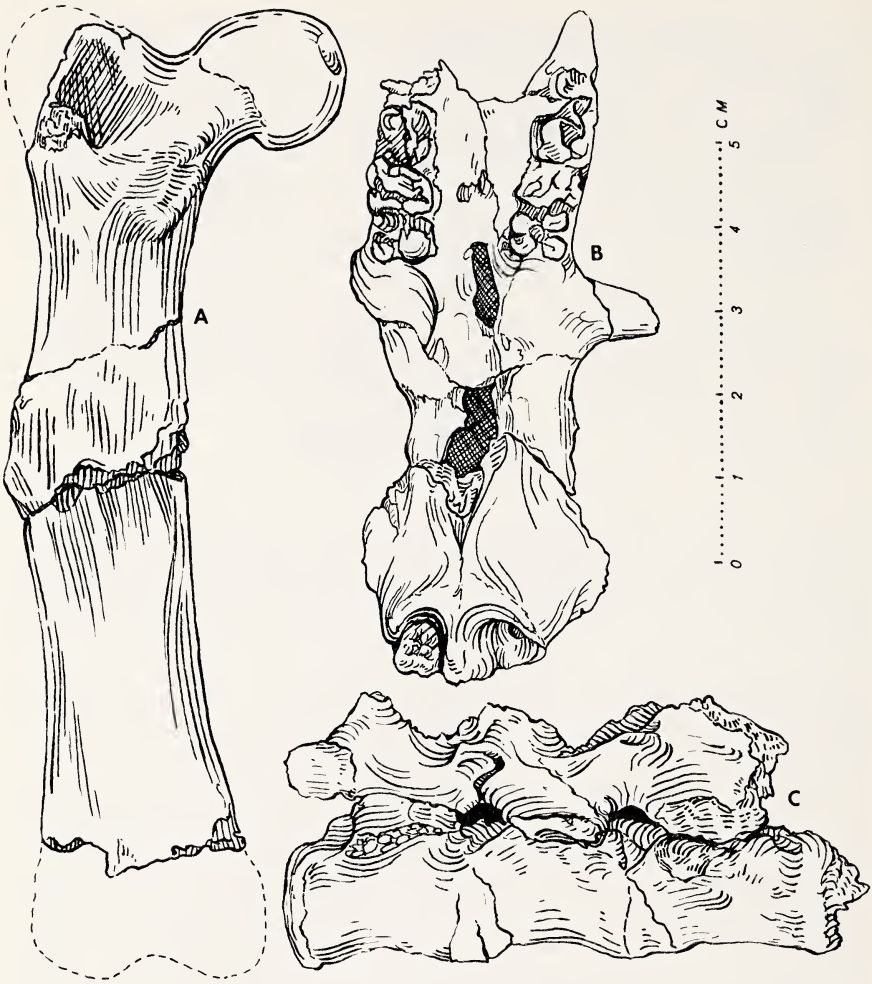



*Figure 3. Coendou stirtoni* n. sp., LACM 6136. Posterior view of left femur (A); ventral view of palate and rostrum (B); and right-lateral view of the sacrum (C).

correct, then it would seem that *C. stirtoni,* like *Erethizon,* did not have a prehensile tail. In living *Coendou* the last caudal to have zygapophyses is the eighteenth (Gupta *ibid.*).

The sacrum (Fig. 3C) in specimen 6136 consists of four fused vertebrae, the neural spines of which are unfused as in adults of living *Coendou* (Gupta *ibid.*).

Named in honor of the late R. A. Stirton.

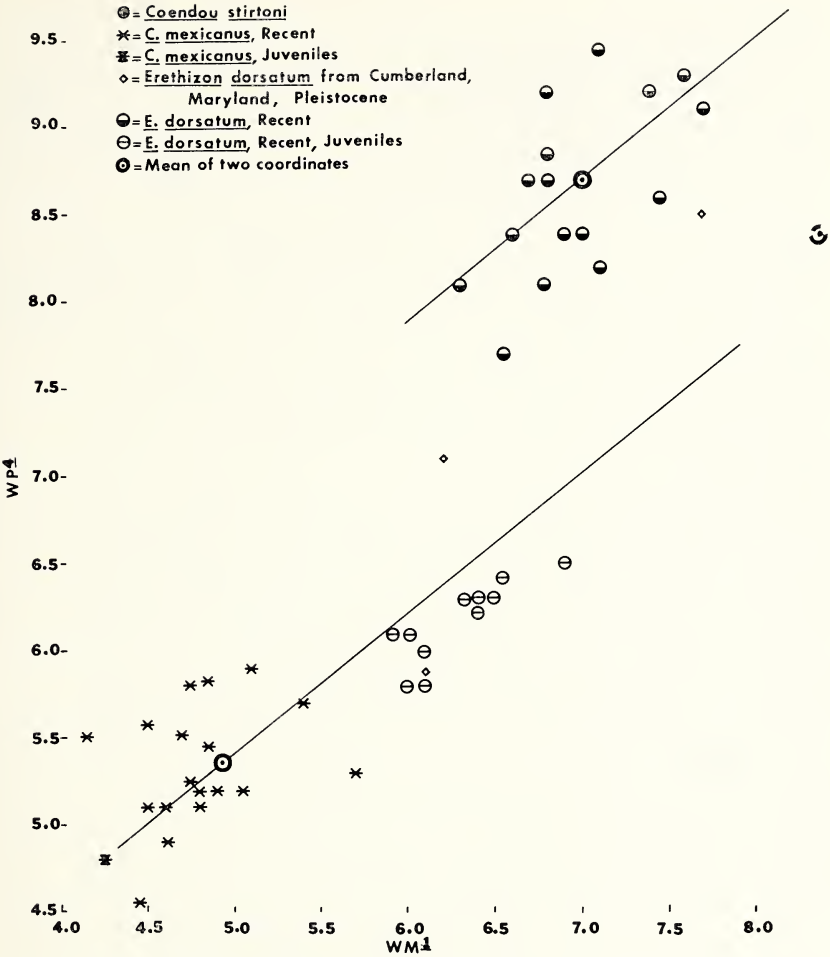



*Figure 4.* Scatter diagram and calculated reduced major axes (diagonal lines) modified from Imbrie (1956) for adults of *Erethizon dorsatum* and *Coendou mexicanus*. The wide separation of the two lines indicates a significant difference between the two samples.

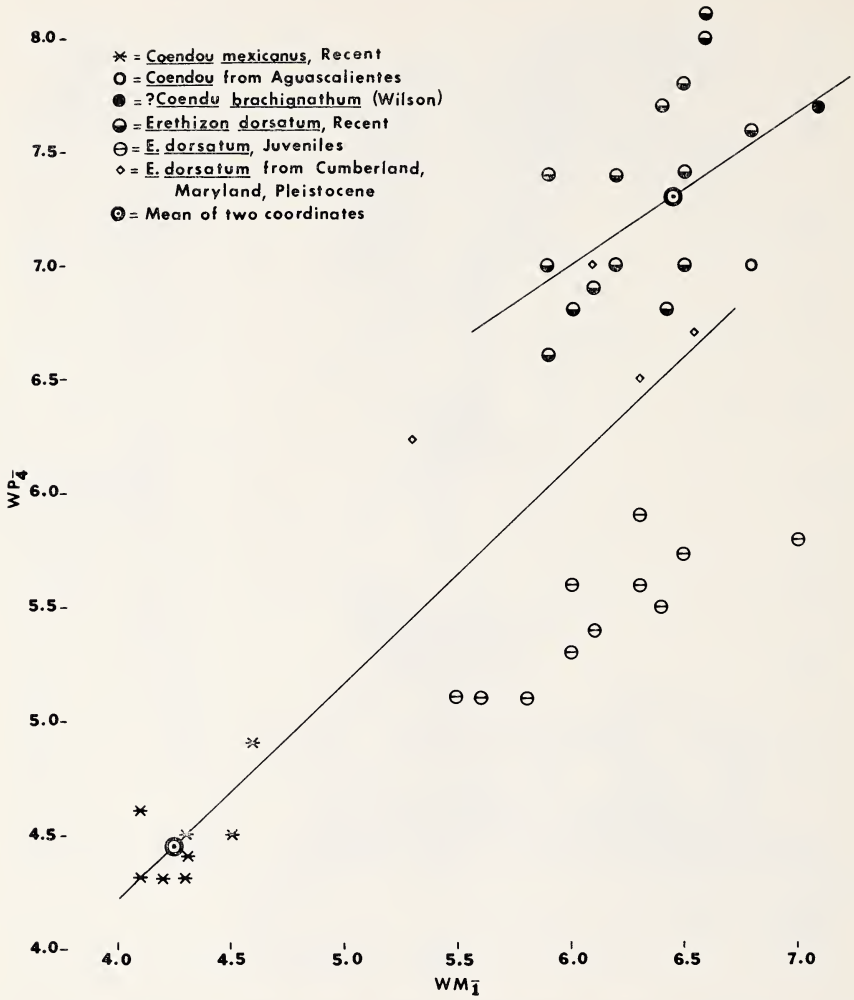



*Figure 5.* Scatter diagram and calculated reduced major axes (diagonal lines) for adults of *Erethizon dorsatum* and *Coendou mexicanus*. See Figure 4 for additional details.

## DISCUSSION

The living species of *Coendou* are adapted to an arboreal habitus, more so than the species of *Erethizon*. The tail in the former is prehensile, while in the latter it is not. It seems likely that *C. stirtoni* had a habitus more like *Erethizon* than the living *Coendou*. The latter inference is based upon the presence of a well-developed third trochanter on the femur, on the presence of zygapophyses only up to the ninth caudal vertebra, and on the large size of *C. stirtoni*.

The degree of divergence posteriad of the upper and lower cheek teeth in adults of *Erethizon* versus the subparallel arrangement of the cheek teeth in *Coendou* (Figs. 6 and 7), seems to reflect a difference in mastication between the two genera. This functional difference can be established as follows:

1. The scratches on the enamel of the occlusal surfaces in both the upper and lower cheek teeth are oriented anteromediad and form an angle greater than 35 degrees with the longitudinal axis of the tooth rows in *Coendou* (Landry 1959). In *Erethizon* this angle is less than 30 degrees (Fig. 8).
2. The angular process of the mandible in adults of *Erethizon* is inflected mediad and the posterolateral surface of the mandible is convex, while in *Coendou* and in juvenile *Erethizon* the angular processes are subparallel and the posterolateral surface of the mandible is flattened.
3. The fossa for the insertion of *M. masseter medialis pars posterior* on the side of the mandible is deeper in *Coendou* than in adults of *Erethizon*. This structure seems related to the degree of inflection of the angular process and to the degree of convexity seen in the posterolateral part of the mandible.
4. The ascending ramus of the mandible in *Coendou* slants posteriad to a greater degree than in adults of *Erethizon*.
5. In adults of *Erethizon* the projection of a line superimposed upon the longitudinal axis of the lower tooth row and bisecting the occlusal surfaces of $P_4$ and $M_3$, passes mediad to the incisor, while in *Coendou* it extends to the posteromedial surface or even laterad to the incisor (Fig. 8). This measurement makes it possible to determine if the mandibular cheek teeth converge as in adults of *Erethizon,* or are subparallel as in *Coendou* and juvenile *Erethizon*.

Juvenile specimens of *Erethizon* have subparallel cheek-tooth rows as well as all the characters mentioned above for the mandibles of *Coendou*. This suggests a paedomorphic relationship between the two genera, in that the adult condition in *Coendou* is found only in the juveniles of *Erethizon*.

In his description of mastication in *Coendou,* Landry (1957: 15) stated, "The teeth occlude on one side at a time, the entire lower jaw pivoting around the condyle on the opposite side. Thus if the stroke begins on the right side the jaw pivots around the left condyle, grinding the right cheek teeth together as

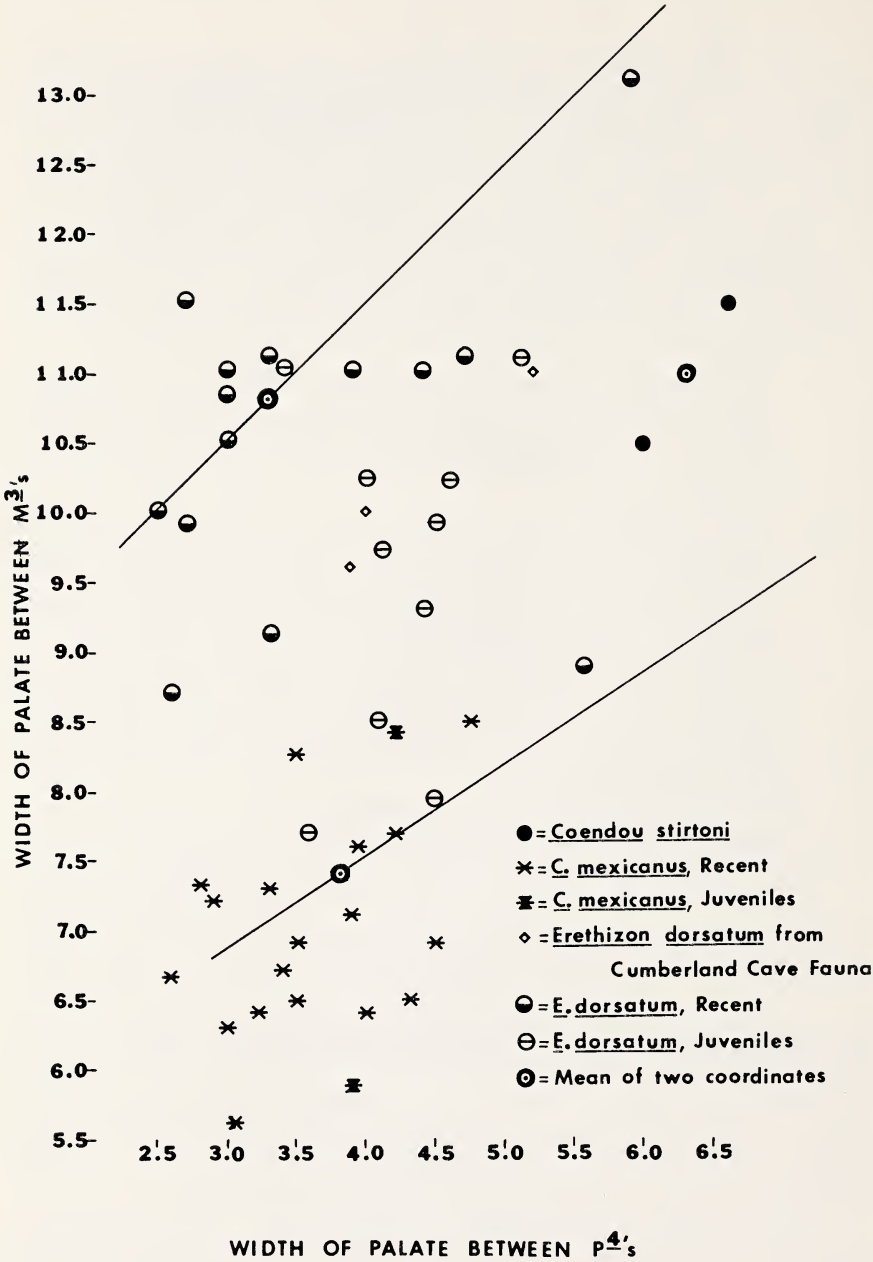



*Figure 6.* Scatter diagram and calculated reduced major axes (diagonal lines) for adults of *Erethizon dorsatum* and *Coendou mexicanus.* See Figure 4 for additional details.

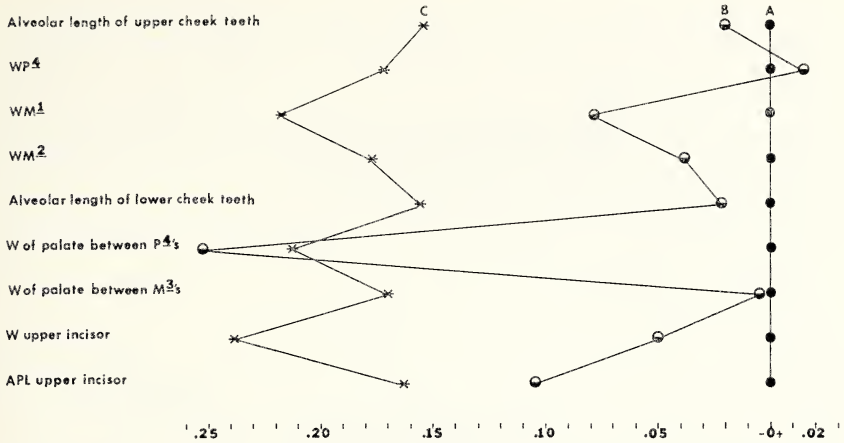



*Figure 7.* Ratio diagrams modified from Simpson *et al* (1960), comparing several cranial dimensions of *Coendou stirtoni* n. sp. (A), with *Erethizon dorsatum* (B), and *Coendou mexicanus* (C). The logs of the means of the dimensions of *C. stirtoni* are assumed to be zero, while the differences between the log of the mean in the latter species (standard) and species being compared are plotted on the positive (+) or negative (—) sides of the zero line.

the right condyle slides forward in the glenoid fossa." In *Erethizon* mastication occurs in a similar manner, but since the teeth in adults of the latter genus converge markedly anteriad, each of the masticatory strokes more closely parallels the longitudinal axis of the tooth row than in *Coendou*, where the tooth rows are subparallel. From the latter it can be inferred that adult *Erethizon* have a more efficient chewing mechanism than either *Coendou* or juvenile *Erethizon*.

Hibbard and Mooser (1963: 247-248) in referring a mandible from the Late Pleistocene (Hibbard *in litt.*) of Aguascalientes, Mexico, to *Erethizon*, noted that their specimen resembled the mandibles in *Erethizon*, except that: "The fossa on the lateral surface and posterior border of the coronoid process for the insertion of *M. masseter medialis, pars posterior* is slightly deeper than observed in the Recent specimens." and "The base of the coronoid process of the fossil does not ascend as vertically as in Recent specimens and therefore makes it possible to see the crowns of the teeth in lateral view." The scratches on the enamel of the occlusal surface of the cheek teeth in this specimen, and the projection of the longitudinal axis of the mandibular cheek teeth, are as in *Coendou* (Fig. 8). This indicates that the specimen (an adult) probably had a masticatory apparatus as in *Coendou* and juvenile *Erethizon*.

The base of the ascending ramus in the mandible described by Wilson (1935) as *Erethizon brachignathum* indicates that it probably sloped posteriad, and the anterior end of the fossa below the coronoid process suggests a condi-

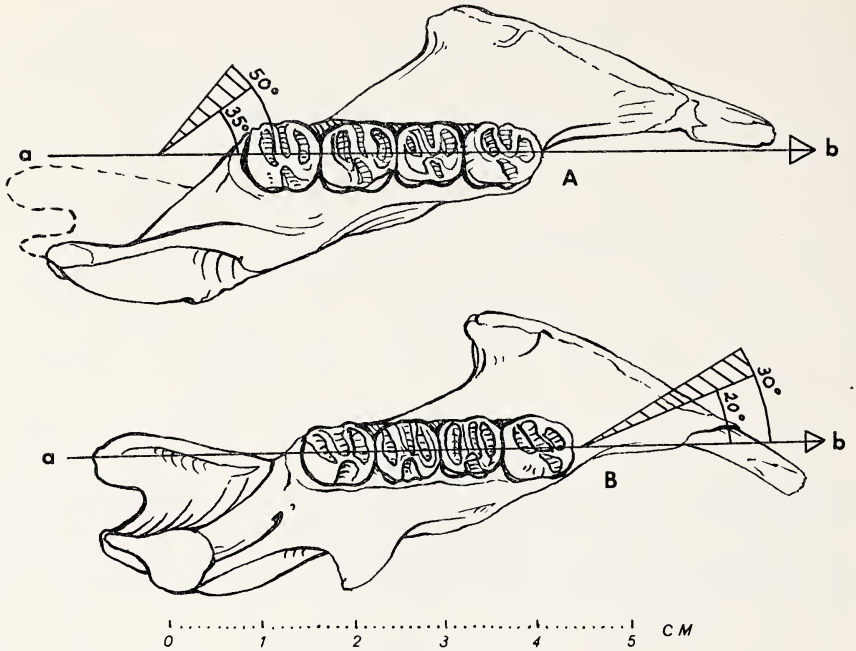



*Figure 8.* Dorsal views of the mandibles of *Coendou* from Aguascalientes, Mexico, UMM V47106 (A), and *Erethizon dorsatum*, USNM 90476 (B). Lines a-b bisect the cheek teeth longitudinally and project as shown by the arrows. The orientation of the scratches on the enamel of the occlusal surfaces of the cheek teeth is indicated by cross-hatching. See text for additional explanation.

tion essentially as in *Coendou*. The orientation of the scratches on the enamel of the cheek teeth of this specimen has not been determined.

In *E. brachignathum* Wilson, the Aguascalientes specimen of Hibbard and Mooser, and the maxillaries of *C. stirtoni*, the cheek teeth closely resemble those in living *Erethizon*. It is difficult to compare the structure of the cheek teeth of living *Coendou* with the above specimens or with those in living *Erethizon*, since the cheek teeth in living *Coendou* are markedly smaller in size, and there is great variability in the cheek-tooth structure of all these forms. The differences in masticatory function between *Coendou* and *Erethizon* are clearcut and seem, consequently, to be of greater importance than dentition in characterizing these two genera.

On functional grounds, then, it seems reasonable to refer tentatively *Erethizon brachignathum* Wilson to ?*Coendou brachignathum* (Wilson), and to refer the specimen from Aguascalientes described by Hibbard and Mooser (1963) to *Coendou*.

The paedomorphic nature of the structures relating to mastication in *Erethizon* strongly suggests that the condition found in adults of *Coendou* and in juveniles of *Erethizon* are primitive and presumably functionally less efficient than the condition found in adult *Erethizon*. Thus, it would seem that *Coendou* is the structural ancestor of *Erethizon*, and that the living species of *Coendou* either are relicts adapted to a narrow niche in the rain forests, or that both genera descended from an unknown, common ancestor in South America. Unfortunately, a fossil record of prehensile-tailed *Coendou* is unknown.

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TABLE 1

Measurements in millimeters of skull parts in *Coendou stirtoni* n. sp.

| | LACM 17633 (Type specimen) | LACM 6136 | LACM 6210A | LACM 6210 |
|---|---|---|---|---|
| Breadth of rostrum lateral to incisors | — | 17.6 | — | — |
| Alveolar length of upper cheek-tooth series | 27.7 | 25.9 | — | — |
| Length of upper diastema from posterior surface of incisor to $P^4$ | — | 39.2 | — | — |
| Width of crown on $P^4$ | 8.4 | — | — | — |
| Width of crown on $M^1$ | 8.4 | — | — | — |
| Width of crown on $M^2$ | 7.8 | — | — | — |
| Alveolar length of lower cheek-tooth series | — | — | 30.7 | — |
| Depth of mandible below $M_2$ | — | 17.7 | 15.8 | 16.7 |
| Breadth of palate between alveoli of $P^4$'s | 6.6 | 6.0 | — | — |
| Breadth of palate between alveoli of $M^3$'s | 11.5 | 10.5 | — | — |
| Width of upper incisor | — | 4.8 | — | — |
| Anteroposterior thickness of upper incisor | — | 6.1 | — | — |

TABLE 2

Measurements in millimeters of skeletal parts in *Coendou stirtoni* n. sp.

| | LACM 6136 | LACM 4325 |
|---|---|---|
| Humerus: distance from medial to lateral epicondyle. | — | 28.2 |
| Ulna: from proximal surface of articular facet of humerus to tip of olecranon process. | — | 11.5 |
| Radius: proximal head: | | |
| Anteroposterior width | 12.8 | — |
| Transverse width | 8.2 | — |
| Femur: from mediolateral base of third trochanter to proximal tip of greater trochanter. | — | 35.3 |
| Anteroposterior width of head | 21.5 | — |
| Astragalus: | | |
| width across trochlea | — | 16.6 |
| greatest anteroposterior length of lateral trochlea | — | 15.2 |
| width of distal articular head | — | 8.6 |
| Calcaneus: | | |
| greatest anteroposterior length | — | 34.5 |
| greatest width | — | 20.1 |
| Cuboideum: from groove of *M. peroneus longus* to lateral margin of antiplantar surface | — | 7.2 |

LOS ANGELES COUNTY MUSEUM

# CONTRIBUTIONS IN SCIENCE

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# SWOLLEN DORSAL FIN ELEMENTS IN LIVING AND FOSSIL *CARANX* (TELEOSTEI: CARANGIDAE)

*By* HARRY L. FIERSTINE

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*Editor*

# SWOLLEN DORSAL FIN ELEMENTS IN LIVING AND FOSSIL *CARANX* (TELEOSTEI: CARANGIDAE)

*By* Harry L. Fierstine[1]

Abstract: Thirty-two specimens of *Caranx hippos* (Linnaeus) and two large specimens each of *C. caballus* Günther, *C. lugubris* Poey, *C. marginatus* Gill, and *C. melampygus* Cuvier from the Gulf of California and the eastern Pacific Ocean were examined for an hypertrophied basal bone of the first dorsal spine. The hyperostoses were found only in specimens of *C. hippos* larger than 343 mm standard length, regardless of sex. The bone is egg-shaped with a deep posterior notch. It is here suggested that this structure may aid in erection of the dorsal fin by increasing the surface area and by changing the direction of pull of the inclinator muscles of the dorsal fin. The element is formed of a thin outer layer of acellular compact bone which surrounds an hypertrophied center of cancellous bone. The cancellous bone is arranged in honeycomblike chambers which are filled with adipose tissue.

Bony elements found in the marine middle Miocene deposits of Sharktooth Hill, Kern County, California, are identified as belonging to *Caranx* sp. and constitute the first record of the genus from the California Miocene. The presence of numerous branching canals, laminae, and lack of honeycomblike chambers eliminate their positive identification as *C. hippos*. The presence of an incipient posterior notch and a more oval shape eliminate their positive identification as *C. carangopsis* Heckel from the Austrian Miocene. This record lends support for assuming a near-shore, tropical or sub-tropical environment for the Sharktooth Hill fauna.

## Introduction

Hyperostosis or hypertrophied bone is often encountered in various parts of the skeleton of perciform fishes (Korschelt, 1940; Schlumberger and Lucké, 1948; Lucké and Schlumberger, 1949; Breder, 1952; Konnerth, 1966). When hyperostosis occurs, it is normally not restricted to one element but is found in more than one area of the skeleton. The structures most commonly affected are the supraoccipital crest and the basal elements of the dorsal and anal fins. In certain species, hypertrophied bony elements are so common that the condition cannot be considered abnormal even though closely related species lack swollen bones (Breder, 1952). The families of fishes that commonly display hyperostoses are the Carangidae (Stein-

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dachner, 1859; Starks, 1911; Korschelt, 1940; Barnard, 1948; Gopinath, 1952; Konnerth, 1966), Ephippidae (Gregory, 1933; Schlumberger and Lucké, 1948; Breder, 1952), Sciaenidae (Chabanaud, 1926), Sparidae (Kesteven, 1928; Takahashi, 1929; Ebina, 1936), and Trichiuridae (Günther, 1860; James, 1960).

The following study reveals the morphology of the swollen dorsal basal elements in the carangid fish, *Caranx hippos* (Linnaeus). This information is applied to the identification of hyperostoses in the marine middle Miocene deposits of Sharktooth Hill, Kern County, California.

## MATERIALS AND METHODS

Thirty-two specimens of *Caranx hippos* (Linnaeus) and two large specimens each of *C. caballus* Günther, *C. lugubris* Poey, *C. marginatus* Gill, and *C. melampygus* Cuvier from the Gulf of California and the eastern Pacific Ocean were examined by dissection or by X-ray photographs. Except for fifteen small specimens of *C. hippos* examined by Mr. Edmund S. Hobson (Zoology Department, University of California, Los Angeles) and discarded in the field, all specimens are contained in the ichthyological collections of the University of California, Los Angeles, or the Los Angeles County Museum of Natural History.

Fossil hyperostoses from the marine middle Miocene deposits of Sharktooth Hill, Kern County, California, are housed in the Vertebrate Paleontology Section of the Los Angeles County Museum of Natural History. Ground thin sections of the fossil bones were prepared by the method described by Enlow and Brown (1956).

## ACKNOWLEDGEMENTS

I wish to thank Dr. Boyd W. Walker and Mr. Wayne Baldwin for the use of the ichthyological collection and equipment at the University of California, Los Angeles. Dr. Shelton P. Applegate, Associate Curator of Vertebrate Paleontology, Los Angeles County Museum of Natural History, offered encouragement and advice as well as access to the paleontological collection. Mr. Frederick H. Berry, Mr. Robert K. Liu, and Drs. David K. Caldwell, Tilly Edinger, and Richard R. Rosenblatt referred me to important literature. Mr. Edward D. Mitchell called attention to examples of fossil hyperostosis, Mr. Dick Bishop gave the Los Angeles County Museum of Natural History fossil hyperostoses from his personal collection, and Mr. Edmund Hobson made observations on 18 *Caranx hippos* at Rancho Buena Vista, Baja California del Sur, Mexico. One recent hyperostosis was stained, sectioned, and photographed through the courtesy of Dr. Marshall R. Urist, M.D., Director of the Bone Research Laboratory, School of Medicine, University of California, Los Angeles. Mr. Armando Solis of the Los Angeles

County Museum of Natural History deserves the entire credit for Figures 2 and 4 and for the printing of Figures 1, 3, and 5.

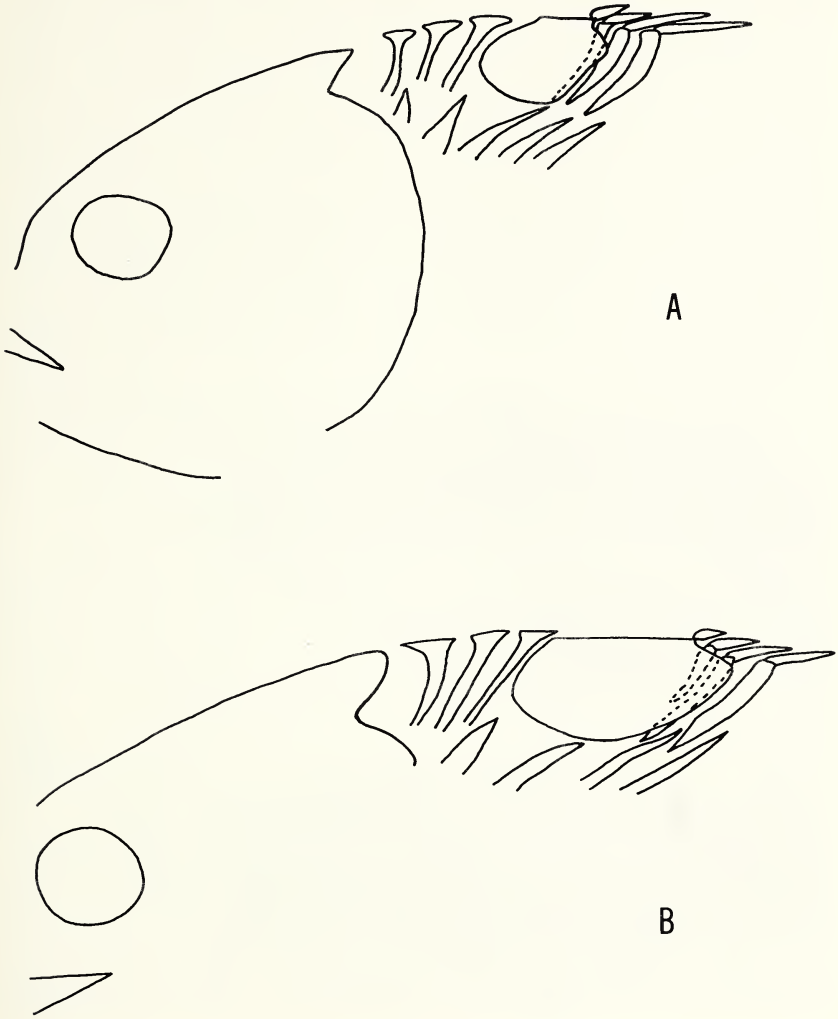


*Figure 1. Caranx hippos* (Linnaeus), tracings from X-ray photographs showing the enlarged basal bone of the first dorsal spine. Note that the hypertrophied bone surrounds the second and third basal elements and is not a fusion of more than one structure. UCLA number W51-21, Mexico, Gulf of California. A. Specimen number 9, Standard length 344 mm, male. B. Specimen number 8, Standard length 425 mm, sex undetermined.

## RESULTS

The basal bone of the first dorsal spine is swollen in all specimens of *Caranx hippos* larger than 343 mm standard length, regardless of sex (Fig. 1). The swollen fin element is absent in 22 smaller specimens (ranging from 170 to 225 mm standard length). The length of the enlarged basal tends to increase linearly with the length of the fish. The excised bone (Fig. 2) is egg-shaped with a deep posterior notch which surrounds the succeeding one or more basal elements of the dorsal fin.

Histological examination reveals a thin outer layer of acellular compact bone which surrounds an hypertrophied center of cancellous bone (Fig. 3). The cancellous bone is formed into a regular network of honeycomblike chambers which are fat filled. In dried preparations, the thin compact layer often cracks and pulls away from the hypertrophied cancellous bone (Fig. 2). No unusual blood vessel or nerve supply was noted.

The great lateral myomeric musculature does not attach to the hyper-

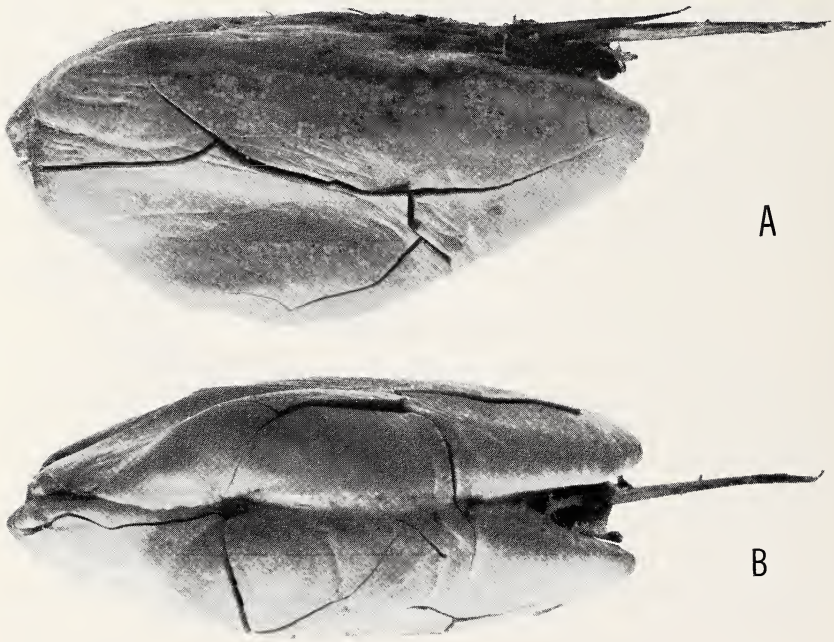


*Figure 2. Caranx hippos* (Linnaeus), basal bone of first dorsal spine, field number 63040203, male, fork length 443 mm, Pacific coast of Costa Rica. Enlarged 1.5 times. A. Left lateral view. Note the thin first dorsal spine which articulates with the swollen basal and the stouter second dorsal spine which is attached to the hypertrophied basal only by ligaments. Additional comments in text. B. Ventral view. Note the deep posterior notch which is partly filled with the basal element of the second dorsal spine.

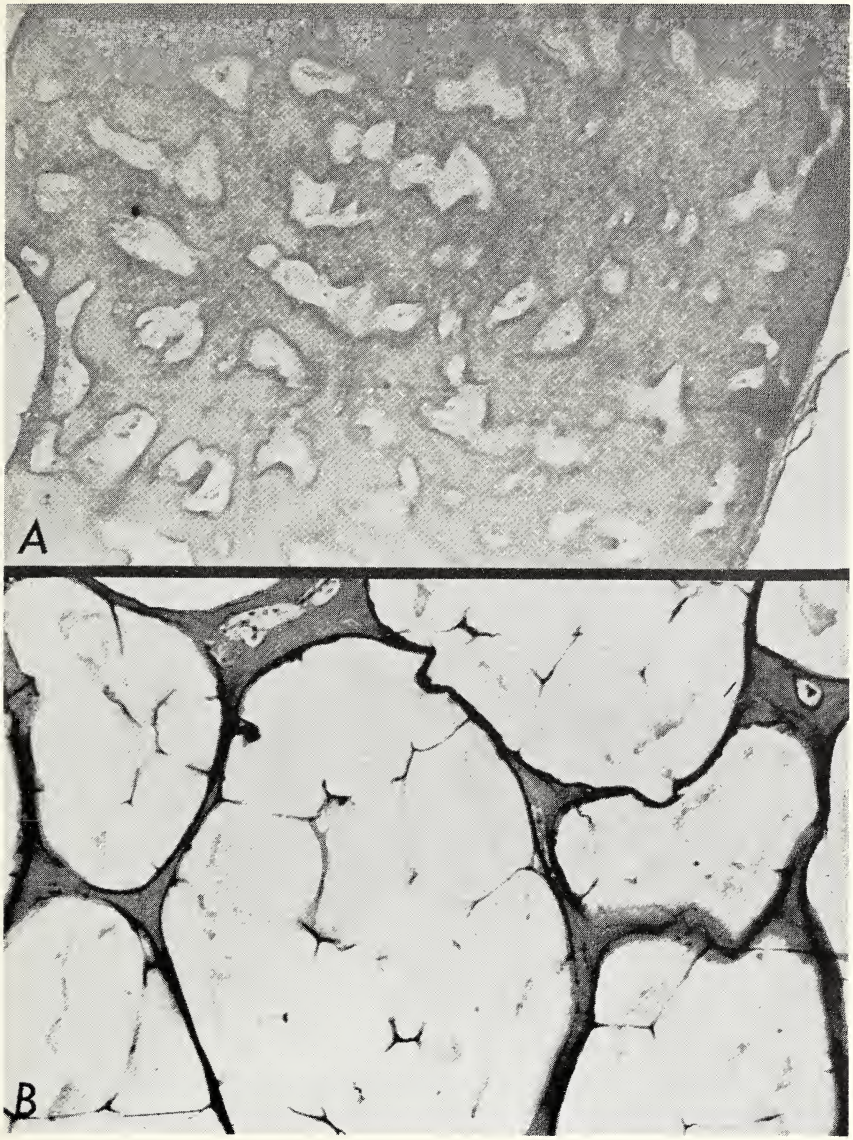


*Figure 3. Caranx hippos* (Linnaeus), longitudinal section of the enlarged basal bone of the first dorsal spine, UCLA number W51-21, specimen number 9, standard length 344 mm, Mexico, Gulf of California. A. Acellular outer compact layer. Enlarged 225 times. B. Acellular inner cancellous layer with adipose tissue enclosed in honeycomb-like chambers. Enlarged 225 times.

*Figure 4. Caranx* sp. Basal bone of first dorsal spine, LACM number $\frac{1557}{16762}$, Middle Miocene, Sharktooth Hill, Kern County, California. Enlarged 2.5 times. A. Left lateral view. B. Ventral view. Note the shallow posterior notch. C. Posterior view. Note the shallow posterior notch.

ostosis, but curves around it. The supracarinales muscle forms a thin anterior layer which originates on the posteriormost free basal and inserts on the anterior midborder of the hyperostosis. The dorsal surface of the swollen basal serves as the point of origin for the inclinator muscles of the first and second spines of the dorsal fin. The inclinator muscles are unusual in two ways: (1) in most fishes they originate from the surface of the great lateral muscles rather than from a bony surface and (2) they normally take a lateral-medial orientation rather than an anterior-posterior direction. These two differences suggest that the enlarged basal may function to erect the dorsal fin by increasing the surface area for the origin of the inclinator muscles of the first and second dorsal spines.

Two large specimens each of *C. caballus, C. lugubris, C. marginatus,* and *C. melampygus* from the eastern Pacific Ocean lacked the enlarged basal bone.

Fossil bones from the marine middle Miocene deposits of Sharktooth Hill, Kern County, California, are readily identified as hypertrophied teleost elements. The shallow posterior notch in the larger bones and the general shape suggest that they are dorsal basal elements of a fish similar to *C. hippos* (Fig. 4).

Ground bone sections reveal a very different histology than that found in recent *C. hippos* (Fig. 5). The compact bone is hypertrophied, laminated, and filled with a lacework of fine canals. These smaller canals interconnect with larger spaces in the cancellous center.

## DISCUSSION AND CONCLUSION

The shape of the hyperostosis, particularly the deep posterior notch, seems to be characteristic for the swollen first dorsal basal in *Caranx hippos.* Starks (1911) mentioned a swollen post-temporal in a 355-mm *C. crysos* (Mitchill) and readily distinguished it from the hypertrophied dorsal bone of a 736-mm *C. hippos.* Steindachner (1859) described the unique shape of the swollen dorsal basal in an 1220-mm *C. carangus* Bloch (= *C. hippos*, see Berry, 1959) and readily distinguished it from swollen ribs, post-temporals, and other swollen bones in the same fish. Gopinath (1952) described the swollen supra-occipital of *C. sexfasciatus* Quoy and Gaimard as peapod-shaped. None of the published figures of swollen elements in other teleost fishes appear similar to the swollen dorsal basal of *C. hippos.*

The histology of the hypertrophied dorsal basal is similar to a figured cross-section of the normal (unswollen) lower jaw of *C. bartholomaei* Cuvier figured by Moss (1961), except for the hypertrophy of the cancellous tissue in *Caranx hippos.*

The function of the swollen basal element is enigmatic. Breder (1952) states that bony growths are never added to a fish as a response to equilibrium or for counter-balancing structures. Furthermore, he noted that they are fat-filled and would not alter the specific gravity. To me, the best functional explanation seems to be that it provides a better mechanism for erection of the dorsal fin. If the growth has a selective advantage (such as surface area for muscle origin), it could not increase linearly with the length of the fish unless it could increase its volume without increasing in weight. This problem could be solved by increasing the cancellous tissue and filling the spaces with buoyant fat, so that an increase in volume would not change the center of gravity for the fish. However, a large *C. hippos* may have other hypertrophied bones (Starks, 1911; Konnerth, 1966), and it is likely that a more complex explanation is necessary to explain the phenomena of hyperostoses.

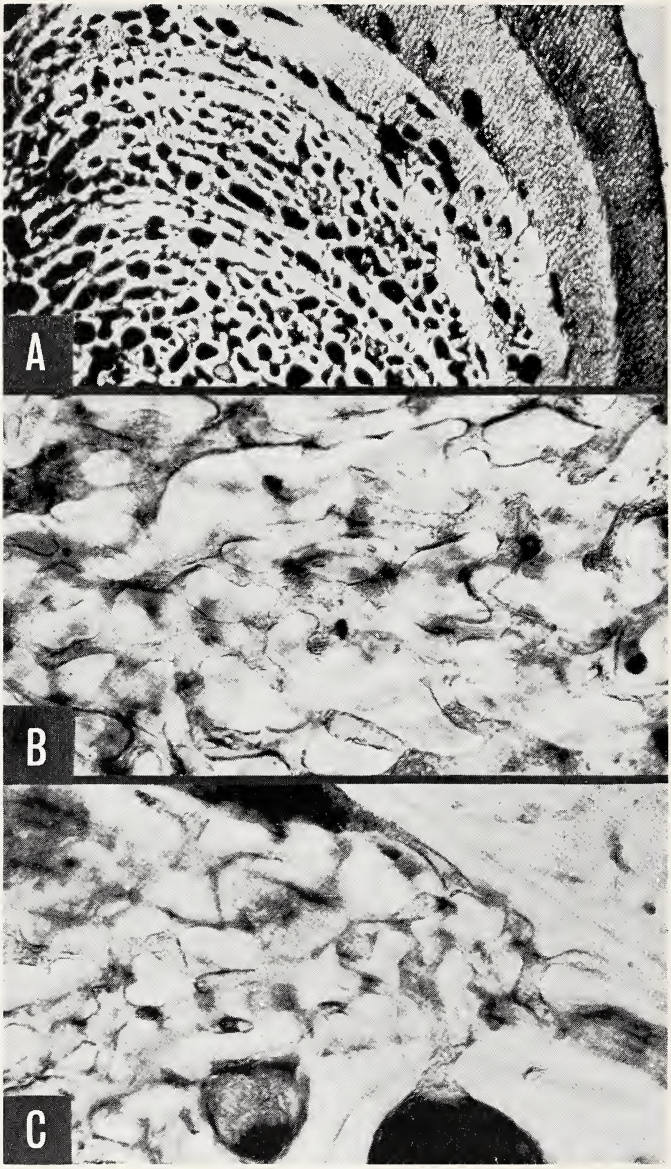


*Figure 5. Caranx* sp. Cross-section of fossil hyperostosis, LACM number $\frac{1655}{16761}$, Middle Miocene, Sharktooth Hill, Kern County, California. A. Outer and inner layers showing small canals, lamellae, and large central spaces. Enlarged 21 times. B. Anastomosing small canals. Enlarged 225 times. C. Inner layer showing anastomosing of large central spaces and small canals. Enlarged 225 times.

The branching tubular network in the fossil bones may have contained fat and may represent an early attempt to increase in volume without increasing the specific gravity. Since the largest fossil hyperostoses are only about one-half the size of those found in living *C. hippos,* it is possible that this method of increasing volume was unsuccessful.

The shape of the fossil hyperostoses from Sharktooth Hill indicate that they belong to the genus *Caranx.* The histological differences detract from their identification as *C. hippos.* Steindachner (1859), in a redescription of *C. carangopsis* Heckel from the Miocene of the Vienna Basin, Austria, described a swollen basal bone. His material was fragmentary and neither his illustrations nor his description indicate a shallow posterior notch. The overall shape may be more spherical than that of the Sharktooth Hill specimens. The type description (Heckel, 1852) is too brief to be helpful. Considering these discrepancies, I choose to identify the hyperostoses as belonging to *Caranx* sp. If reexamination of the Austrian material shows a similar histology, then the Sharktooth Hill specimen should be considered as belonging to *C. carangopsis.*

Since most living species of *Caranx* are restricted to near-shore tropical and subtropical waters, a similar environment for the Sharktooth Hill fauna is suggested. Other piscine evidence (Applegate and Fierstine, unpublished data) supports this supposition.

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# REVIEW OF THE LANTERNFISH GENUS *LAMPADENA* WITH A DESCRIPTION OF A NEW SPECIES

*By* BASIL G. NAFPAKTITIS AND JOHN R. PAXTON

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# REVIEW OF THE LANTERNFISH GENUS *LAMPADENA* WITH A DESCRIPTION OF A NEW SPECIES

*By* Basil G. Nafpaktitis[1] and John R. Paxton[2]

Abstract: The genus *Lampadena,* family Myctophidae, includes seven known species, one of which, occurring in the southern hemisphere, is here described as new. We consider *L. nitida* to be conspecific with *L. luminosa* and do not recognize the subgenus *Lychnophora.* The otoliths of the species in the genus show interspecific differences, and thus are of taxonomic value. The distribution of each species is plotted and tentative conclusions concerning relationships within the genus are presented.

## Introduction

In spite of the considerable amount of work which has been done on the family Myctophidae, many groups within the family need to be reworked. There are three reasons for this: (a) inadequate original and subsequent descriptions, including, as Bolin (1959) has emphasized, extremely general statements concerning the distribution of individual species; (b) addition of new species; and (c) the potential for more critical comparative studies due to the increase in the number and size of collections.

Prior to Bolin's work (1959) the genus *Lampadena* comprised a total of nine described species assigned by Fraser-Brunner (1949) to two subgenera, *Lampadena* and *Lychnophora.* Two of these nine species were placed by Bolin in a separate genus, *Taaningichthys.* Further, the same author placed *Lampadena braueri* Zugmayer in the synonomy of *L. speculigera* Goode and Bean. Paxton (1963) described a new species, *L. urophaos,* from the eastern north Pacific, and placed it in the subgenus *Lychnophora.* At that point the composition of the two subgenera was as follows: subgenus *Lampadena—L. speculigera, L. dea, L. chavesi, L. anomala;* subgenus *Lychnophora—L. luminosa, L. nitida, L. urophaos.*

The two main purposes of the present work are (a) to bring "under one roof" detailed descriptions of all the species of the genus found scattered in the literature, and (b) to present a survey of those species which occur in the southern oceans. The genus as a whole is rather uncommon. Examination of many more collections around the world will probably result in an increase in the number of known species in the genus and further elucidate individual patterns of distribution. With representatives of all currently known species

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available to us, we thought it advisable to redescribe them in as much detail as possible, thus hoping to minimize confusion in future investigations.

## MATERIALS AND METHODS

The ultimate rays of the dorsal and anal fins are double, but they have here been considered as single. Only the well-developed gill rakers of the first gill arch (one side) have been counted. In the method of taking measurements and presenting data we follow Bolin (1939). A few modifications and additions were made, however. These are as follows: depth of body—the vertical through the upper end of the base of the pectoral fin; caudal peduncle length—the distance from the base of the last anal ray to the end of the hypural plate; caudal gland length—the greatest extent of the luminous tissue, not always a midline measurement. Most measurements and proportionality data have proven unsatisfactory for the elucidation of differences between species of the genus *Lampadena*. Rather than present what we consider meaningless data under each species description, those measurements which have proven useful are summarized in Table 1. Certain proportions, notably the lengths of the dorsal and anal fin bases, have been utilized in the past to characterize genera. To enable a future comparison of the genus *Lampadena* with other myctophid genera, those measurements, expressed as per cent of standard length (SL), which are not useful at the specific level, are summarized for all species (except *L. anomala*) as follows: length of head, 28.4-36.6; depth of head, 18.2-23.3; length of upper jaw, 19.1-26.9; depth of body, 18.3-23.8; predorsal distance, 44.3-50.0; prepectoral distance, 28.9-37.4; preventral distance, 40.9-50.5; preadipose distance, 69.2-78.8; length of base of dorsal fin, 12.6-20.7; length of base of anal fin, 11.8-16.7. A list of individual measurements and calculated percentages of standard lengths for all specimens is available on request. Vertebral counts and structure were determined from X-rays.

Under the description of each species, locality data are presented for all specimens examined and ranges of standard lengths are given. Coordinates for the starting position only of each trawl are included. All time is in local time. All captures were made with a 10′ Isaacs-Kidd Midwater Trawl (IKMT), unless otherwise indicated. For open IKMT captures, the depth sampled is recorded from the surface to maximum depth reached by the gear. For captures with an IKMT equipped with a closing device, the discrete depth sampled is indicated.

The terminology of body photophores is that of Bolin (1939). Consistent within all specimens examined, and indeed in the entire family, is the presence of three Br photophores on the branchiostegal membranes under the ventral sheet of the dentaries. Since they are invariably present, their occurrence is omitted from the species descriptions.

Otoliths were measured with an ocular micrometer, then lightly smeared

with graphite to bring out details in their sculpture and photographed. The entire series of otoliths is deposited in the extensive collection established by John Fitch of the California Fish and Game at Terminal Island and supported by a National Science Foundation Grant. The terminology on otoliths follows that of Frizzell and Dante (1965).

## KEY TO THE SPECIES OF THE GENUS *Lampadena*

1a. None of the PO abruptly and highly elevated ..... 2

1b. $PO_4$ abruptly and highly elevated, about over $PO_3$ ..... *L. luminosa* (Garman, 1899)

2a. VO plus SAO 7-9; AOa 5-7; Pol immediately below or very close to lateral line ..... 3

2b. VO plus SAO 5-6; AOa 3-4; distance between Pol and lateral line about half as great as that between Pol and ventral contour of caudal peduncle ..... *L. anomala* Parr, 1928

3a. $Prc_1$-$Prc_2$ interspace equal to, or greater than, three times the diameter of a photophore of this series ..... 4

3b. $Prc_1$-$Prc_2$ interspace much shorter than three times the diameter of a photophore of this series ..... 5

4a. Last two (sometimes three) AOa entirely behind base of anal fin; two AOp; infracaudal luminous gland very long, at least 1.5 times as long as least depth of caudal peduncle, almost twice as long as diameter of eye; crescent-shaped patch of whitish tissue on iris above pupil; pterotic spine directed posteriorly ..... *L. chavesi* Collett, 1905

4b. No AOa behind base of anal fin; four to five AOp (rarely three); infracaudal luminous gland shorter than 1.5 times the least depth of caudal peduncle and about 1.5 times as long as diameter of eye; no crescent-shaped patch of whitish tissue on iris above pupil; pterotic spine directed downward and forward (in specimens longer than about 30 mm) ..... *L. dea* Fraser-Brunner, 1949

5a. Gill rakers 6-8+1+12-17; supracaudal gland shorter than infracaudal gland; mesopterygoid teeth uniformly small ..... 6

5b. Gill rakers 3-5+1+8-10; supracaudal gland equal in length to or somewhat longer than infracaudal gland; posterior mesopterygoid teeth noticeably enlarged ..... *L. urophaos* Paxton, 1963

6a. Distance between posterior end of base of anal fin and anterior margin of infracaudal gland equal to, or slightly greater than, length of this gland; photophores small, in specimens smaller than 30 mm AOa about two organ diameters apart from each other; first and usually second AOp in front of infracaudal gland; AOa level; gill rakers 6-7+1+12-14, total

19—22.....*L. speculigera* Goode & Bean, 1896

6b. Distance between posterior end of base of anal fin and anterior margin of infracaudal gland equal to about one-fourth of length of this gland; photophores large, in specimens smaller than 30 mm AOa less than one organ diameter apart from each other; all AOp well over infracaudal gland; last AOa usually distinctly raised above level of rest of organs of same series; gill rakers 7-8+1+16-17, total 24-26.....*L. notialis* sp. n.

**Lampadena luminosa** (Garman, 1899)

Fig. 1

R/V ANTON BRUUN, cruise III, sta. 147, 06°54′N, 59°55′E, 16 August 1963, 1845-2213 hrs, depth sampled 0-750 m, bottom depth 1775-3015 m, one specimen, 31.0 mm; sta. 151, 04°52′S, 60°02′E, 23 August 1963, 0625-1350 hrs, depth sampled 0-2030 m, bottom depth 3895 m, two specimens, 67.5-86.0 mm.

R/V ANTON BRUUN, cruise VI, sta. 334A, 06°01′N, 64°59′E, 24 May 1964, 1912-2345 hrs, depth sampled 0-700 m, bottom depth 4663 m, one specimen, 53.0 mm; sta. 335B, 03°46′N, 65°05′E, 26 May 1964, 0100-0850 hrs, depth sampled 0-275 m, bottom depth 2926 m, two specimens, 39.5-49.0 mm; sta. 341B, 07°56′S, 65°14′E, 1-2 June 1964, 2200-0300 hrs, depth sampled 0-504 m, bottom depth 4200 m, one specimen, 22.0 mm; sta. 342A, 09°57′S, 64°55′E, 2 June 1964, 1755-2250 hrs, depth sampled 0-525 m, bottom depth 3200 m, 12 specimens, 16.5-29.0 mm; sta. 343A, 12°10′S, 64°54′E, 4 June 1964, 0020-0510 hrs, depth sampled 0-798 m, bottom depth 3200 m, one specimen, 20.0 mm; sta. 345E, 17°58′S, 65°34′E, 7 June 1964, 2130-2400 hrs, depth sampled 0-120 m, bottom depth 3000 m, five specimens, 17.0-22.0 mm.

Scripps Institute of Oceanography, SIO 60-239-25H, 04°56′N, 142°54′W, 6 July 1960, one specimen, 22.5 mm.

R/V ATLANTIS II, cruise 13, sta. RHB 1005, 41°26′N, 59°01′W, 4 September 1964, 1045-1410 hrs, depth sampled 0-555 m, one specimen, 28.0 mm; sta. RHB 1013, 41°36′N, 52°21′W, 6 September 1964, 1940-2320 hrs, depth sampled 0-65 m, one specimen, 23.5 mm.

R/V CHAIN, cruise 17, sta. RHB 801, 00°15′S, 18°40′W, 26 April 1961, 0250-0605 hrs, depth sampled 0-85 m, one specimen, 49.0 mm.

R/V CHAIN, cruise 35, sta. RHB 960, 07°39′N, 45°14′W, 11 February 1963, 2005-2350 hrs, depth sampled 0-60 m, one specimen, 27.0 mm; sta. RHB 966, 01°13′S, 34°35′W, 17 February 1963, 0335-0605 hrs, depth sampled 0-102 m, four specimens, 23.0-33.0 mm.

R/V CHAIN, cruise 60, sta. RHB 1252, 16°45′N, 64°18′W, 24 May 1966, 2015-2335 hrs, depth sampled 0-84 m, 12 specimens, 19.0-33.0 mm; sta. RHB 1253, 16°38′N, 64°27′W, 25 May 1966, 0046-0400 hrs, depth sampled

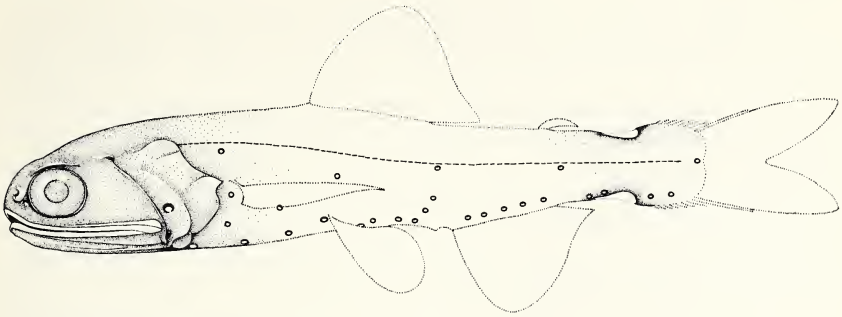

Figure 1. *Lampadena luminosa*, 67.4 mm in standard length; 04° 52′ S, 60° 02′ E.

0-133 m, two specimens, 20.0-27.0 mm; sta. RHB 1258, 13°32′N, 71°24′W, 27 May 1966, 2030-2300 hrs, depth sampled 0-210 m, one specimen, 19.0 mm; sta. RHB 1261, 13°04′N, 73°12′W, 28 May 1966, 1628-1955 hrs, depth sampled 0-300 m, four specimens, 29.0-66.0 mm; sta. RHB 1263, 12°58′N, 73°34′W, 29 May 1966, 0040-0450 hrs, depth sampled 0-120 m, nine specimens, 27.0-69.0 mm; sta. RHB 1286, 19°46′N, 83°07′W, 10 June 1966, 0020-0505 hrs, depth sampled 0-86 m, nine specimens, 17.0-51.0 mm; sta. RHB 1289, 21°11′N, 85°12′W, 10 June 1966, 2010-2320 hrs, depth sampled 0-170 m, two specimens, 41.5-64.0 mm; sta. RHB 1290, 21°17′N, 85°22′W, 11 June 1966, 0030-0400 hrs, depth sampled 0-124 m, eight specimens, 17.0-71.0 mm (otolith of 71.0 mm specimen photographed, Fig. 10); sta. RHB 1307, 27°01′ N, 90°02′W, 22 June 1966, 0007-0400 hrs, depth sampled 0-95 m, six specimens 39.0-67.5 mm; sta. RHB 1315, 25°46′N, 79°47′W, 25-26 June 1966, 0002-0400 hrs, depth sampled 0-71 m, 41 specimens, 18.0-26.0 mm.

D. 15; A. 14(13-15); P. 16(15-17); V. 8; gill rakers 4+1+9(8-10), total 14(13-15); PO 5; VO 4-5; AOa 5-6 (rarely 7); AOp 2; Prc 2+1; lateral line scales 35-37; vert. 36(37), 8 x-rayed specimens. Of 16 specimens counted, only one had P. 17.

A relatively large myctophid fish; snout obtuse and round; mouth large, terminal, its cleft somewhat oblique; eye of moderate size, its diameter 3.7 to 4.3 in length of head; opercular margin concave posterodorsally, convex posteroventrally, tapering into a rather sharp point located above $PVO_2$ and with a distinct indentation at about level of same organ; pterotic spine strong and directed posteriorly.

Origin of dorsal fin distinctly in advance of vertical through base of outermost ray of ventral fin; origin of anal fin well behind vertical through end of base of dorsal fin; base of adipose fin somewhat in advance of vertical through end of base of anal fin; pectoral fin long, extending to level of second or third VO; ventral fin reaching anus.

A small, roundish Vn posteroventrad to nasal apparatus, capped by crescent-shaped, darkly pigmented tissue; a narrow strand of black tissue extending along entire anterior margin of orbit. A very small, deeply embedded $Op_1$ close behind angle of mouth; $Op_2$ larger than general body photophores, directly over or slightly posterior to $Op_1$ and about at level of ventral margin of orbit.

PLO in advance of base of pectoral fin and 1.5 to 2 times its own diameter below lateral line. $PVO_1$ at about level of posterior end of maxillary and somewhat in advance of vertical through $PVO_2$; $PVO_2$ somewhat behind straight line connecting PLO with $PVO_1$, distinctly above level of $Op_2$ and in front of middle of base of pectoral fin. First PO interspace 1.2 to 1.4 times as wide as second, which is equal to or somewhat narrower than that between $PO_3$ and $PO_5$; $PO_5$ displaced laterally, situated about its own diameter in front of and anteromesad to base of outermost ray of ventral fin; $PO_4$ highly and abruptly elevated, over, slightly anterior or slightly posterior to vertical through $PO_3$ and on same level with, or somewhat higher than, $PVO_1$. VLO distinctly behind vertical through base of outermost ray of ventral fin and somewhat nearer to lateral line than to base of ventral fin. VO series forming a gentle arc; $VO_1$ posteromesad to base of inner ray of ventral fin. SAO slightly angular, with last VO, $SAO_1$ and $SAO_2$ equidistant and on straight, steeply ascending line; $SAO_2$-$SAO_3$ interspace about twice as wide as $SAO_1$-$SAO_2$ interspace; $SAO_3$ on or slightly posterior to vertical through $SAO_2$ and immediately below lateral line. AOa level and usually evenly spaced. Pol behind vertical through last AOa and immediately below lateral line. $AOp_1$ slightly in front of, or directly over anterior end of infracaudal luminous gland and separated from $AOp_2$ by a distance about 1.5 times the diameter of these organs. $Prc_1$ and $Prc_2$ on horizontal line, space between them varying from 1 to 2.5 times the diameter of these organs; $Prc_3$ at base of middle rays of caudal fin, on level of lateral line and well behind vertical through $Prc_2$.

Supra- and infracaudal luminous glands of about equal length, somewhat shorter than diameter of eye; distance between anterior end of infracaudal gland and posterior end of base of anal fin about equal to or slightly less than length of gland.

Several series of needlelike teeth on both jaws, those of inner series distinctly larger and more widely spaced; four to five large, recurved teeth directed anteriorly at posterior end of dentary; one to two large teeth hooked forward in inner dentary row near symphysis (these peculiar teeth are undifferentiated in young specimens and often missing in large ones); anteriormost premaxillary teeth in outer row very slightly hooked. Palatines with a narrow band of small teeth. A small patch of similar teeth on distal end of each limb of vomer. Mesopterygoid teeth in large patch with medial series greatly enlarged in maturing fish (about 65 mm), undifferentiated in size in young individuals; last few teeth on posterolateral margin of patch also enlarged. Quite often, in

the fish examined, several specimens of comparable size from the same haul showed marked differences in the development of the medial series of mesopterygoid teeth.

Neural arches of anterior vertebrae not greatly expanded.

A direct comparison of the type specimens of *Lampadena luminosa* and *L. nitida* (Tåning, 1928) revealed no differences. Tåning, it seems, established his subspecies *L. luminosa nitida* mainly on the basis of the division of the VO series into two groups (Bolin, pers. comm.). A grouping of the VO into 1+1+3 is clearly visible in Garman's type. Furthermore, examination of several specimens, from both the Atlantic and Indian Oceans, shows that irregularities in the spacing of both the VO and the AOa series are not uncommon within a given population. Some specimens have five VO evenly spaced, others, from the same station, have the same number of VO but the series is divided into two groups (2+3). Still others possess only four VO either evenly spaced or with the $VO_2$-$VO_3$ interspace distinctly wider than the other interspaces in the series. Finally, in some cases where there are five VO, the third is markedly reduced in size. With these differences appearing to be a simple expression of intra-specific variation and with no other differences sharp enough to justify the establishment of two species, or even subspecies, we place Tåning's *L. luminosa nitida* in the synonymy of *L. luminosa* Garman.

It should also be added here that among the Indian Ocean specimens two trends involving the numbers and arrangement of the VO, AOa and Prc can be discerned. Specimens with four VO usually, but not invariably, have five AOa. The $Prc_1$ and $Prc_2$ in these specimens are separated by a distance equal to 2 to 2.5 times the diameter of a body photophore. On the other hand, specimens with five VO tend to have six AOa. The $Prc_1$-$Prc_2$ interspace in the latter individuals is equal to 1 to 1.5 times the diameter of a body photophore. Intermediates between the two patterns are not uncommon and the differences in the three characters mentioned seem to intergrade.

*Lampadena luminosa* appears to be a tropical species, found mainly in equatorial waters of all three oceans, between 20°N and 20°S (Fig. 8). Its occurrence in the Gulf of Mexico, Straits of Florida and high latitudes in the western north Atlantic is probably due to the influence of the Gulf Stream. Individuals of many tropical myctophid species have often been taken all along the path of this current as far as 42°N in the western half of the north Atlantic (O'Day and Nafpaktitis, 1967). It is reasonable to suspect a similar situation in the western north Pacific. For instance, Matsubara (1952) reports, under the name *L. nitida,* a specimen 150 mm (SL) taken by commercial fishermen off Owase, Mie Prefecture, Japan.

### **Lampadena urophaos** Paxton, 1963

Fig. 2

Most of the examined specimens are from the southern California off-

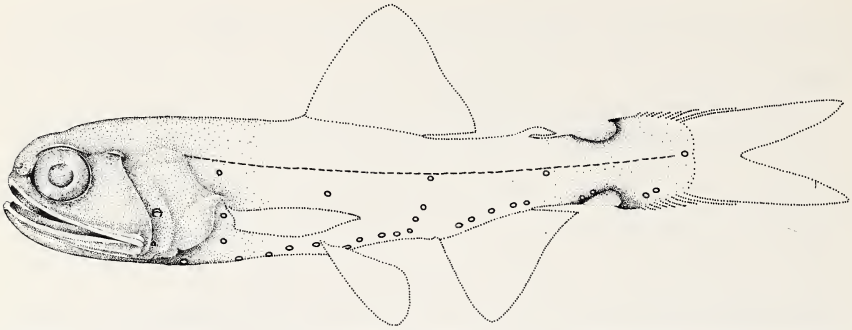

Figure 2. *Lampadena urophaos*, 56.0 mm in standard length; San Nicolas basin, California.

shore waters, and only a few localities were plotted (Fig. 9). Station data for the Pacific localities are from Berry and Perkins (1966), Paxton (1963), and Pearcy (pers. comm.); coordinates for the latter are 34°49′N, 160°19′W, and 42°00′N, 126°59′W. The following Atlantic specimens were also examined: CAP'N BILL III, sta. RHB 910, 38°24′N, 71°08′W, 12 October 1962, 1330-1830 hrs, 0-713 m, 64′ midwater trawl, one specimen, 73.6 mm; R/V CHAIN, cruise 49, sta. RHB 1111, 21°33′N, 70°12′W, 17 June 1965, 1520-1940 hrs, 612-668 m, two specimens, 19.0-22.7 mm.

D. 15(14-16); A. 14(13); P. 16(15-17); V. 8; gill rakers 4(3-5)+1+8-9(10), total 13-14(16); PO 5; VO 5(4-6); AOa 5(6); AOp 2(3); Prc 2+1; lateral line scale pockets 37; vert. 36(35), 6 x-rayed specimens. Of 22 specimens examined, the following counts were observed only once: D. 16; P. 17; gill rakers 3+1+9, 5+1+10; VO 6; AOa 6; AOp 3.

Snout bluntly rounded; mouth large, terminal, its cleft slightly oblique; eye moderate in size, its diameter 3.5 to 4.1 in length of head; posterior opercular margin produced into a point situated above $PVO_2$; pterotic spine strong, directed posteriorly and slightly ventrally.

Origin of dorsal fin distinctly anterior to origin of ventral fin; origin of anal fin behind vertical through end of base of dorsal fin; base of adipose fin somewhat in advance of vertical through end of base of anal fin; pectoral rays extending about to level of $VO_2$; ventral rays almost reaching origin of anal fin.

Vn small, posterior and ventral to nasal organ; anterior margin of orbit, from below Vn to above nasal organ, lined with black tissue. $Op_1$ small and difficult to discern, situated about on same level as and close behind posterior end of maxillary; $Op_2$ larger than body photophores, located about at level of ventral margin of orbit, slightly behind vertical through $Op_1$.

PLO one to three photophore diameters below lateral line and anterior to $PVO_2$. $PVO_2$ slightly anterior to upper half of base of pectoral fin; $PVO_1$ about on level of posterior end of mouth, slightly anterior to or under $PVO_2$ in

Pacific specimens and under or slightly posterior to $PVO_2$ in Atlantic specimens. First PO interspace about twice as wide as others; $PO_2$ to $PO_5$ evenly spaced or $PO_4$-$PO_5$ interspace slightly larger; $PO_1$ to $PO_3$ in a horizontal line, with $PO_4$ and $PO_5$ diverging posteriorly; $PO_4$ somewhat closer to level of $PO_5$ than to that of $PO_3$; $PO_5$ slightly anteromesad to base of outermost ray of ventral fin. VLO distinctly behind vertical through base of outermost ray of ventral fin, closer to lateral line than to base of ventral fin. $VO_1$ slightly posteromesad to base of innermost ray of ventral fin; rest of VO somewhat higher, the entire series forming a gentle arc, with the organs evenly spaced or with $VO_2$-$VO_3$ interspace largest, particularly if only four VO present. Last VO, $SAO_1$ and $SAO_2$ evenly spaced and in a straight line; $SAO_3$ over or slightly posterior to $SAO_2$, about under base of last dorsal ray and immediately below lateral line; $SAO_2$-$SAO_3$ interspace about twice as wide as others in series. AOa in a straight line, evenly spaced or noticeably grouped (2+1+2); last AOa directly over or slightly anterior to base of last anal ray. Pol behind last AOa, immediately below lateral line. $AOp_1$ over anterior margin of infracaudal gland, separated from $AOp_2$ by 1 to 1.5 photophore diameters (in the one specimen with three AOp, the third is half the size of other body photophores). $Prc_1$ over second or third ventral procurrent spine, one to two photophore diameters anterior to $Prc_2$; $Prc_3$ at base of middle rays of caudal fin and slightly above level of lateral line.

In small specimens, supra- and infracaudal luminous glands are about equal in length; in all large Pacific specimens (over 50 mm), the supracaudal gland is somewhat longer, while they are of equal length in the large Atlantic specimen; distance from base of last anal ray to anterior margin of infracaudal gland two-thirds to one times the length of infracaudal gland.

Premaxillary and dentary with wide band of conical, closely-set teeth; entire inner row of dentary composed of larger, more widely-spaced conical teeth; three to five large, recurved teeth directed anteriorly at posterior end of dentary; inner row of premaxillary teeth only slightly enlarged; dentigerous portion of premaxillary, near symphysis, somewhat widened to form an approximately triangular area, with an upper (outer) row of three to five large, recurved teeth directed posteroventrally. A narrow band of small teeth along length of palatine. A small patch of teeth on distal ends of vomer. Very small mesopterygoid teeth in an elongated, oval-shaped patch; posterolateral margin of patch with row of six to ten moderate-size teeth.

Neural arches of anterior vertebrae not greatly expanded.

A number of errors were made in the original description (Paxton, 1963), which are corrected in the above description. The antorbital organ, which is difficult to discern in adult specimens and is obscured by the black tissue at the anterior portion of the orbit, is definitely ventral to the nasal organ. Thus, *L. urophaos* agrees with all of its congeners in the presence of a small Vn. The ventral ray count for the species is eight, plus a small accessory splint on the

base of the first ray. With very few exceptions (notably species in the genera *Gonichthys* and *Notolychnus*), eight ventral rays plus an accessory splint is constant for the family Myctophidae. The $PO_4$ and $PO_5$, while slightly raised out of the line of $PO_1$-$PO_3$, are not as highly elevated as is the $PO_4$ in *L. luminosa. L. urophaos* can therefore be referred to the subgenus *Lampadena,* as defined by Fraser-Brunner (1949). The status of the subgenus *Lychnophora* will be discussed after the species descriptions.

*Lampadena urophaos* occurs between 25°N and 42°N in the central and eastern Pacific and between 21°N and 38°N in the western Atlantic (Fig. 9). The minor differences noted between the Pacific and Atlantic populations, namely the position of the $PVO_1$ and the relative sizes of the caudal glands, may be expected in widely allopatric populations. A more complete comparison of the populations must await the collection of additional large Atlantic specimens.

### **Lampadena speculigera** Goode and Bean, 1896

Fig. 3

USNS ELTANIN, cruise 15, sta. 1402, 39°15′S, 179°35′W, 30 November to 1 December 1964, 2353-0600 hrs, depth sampled 0-2489 m, bottom depth 2946-3514 m, one specimen, 20.0 mm.

USNS ELTANIN, cruise 23, sta. 1710, 41°44′S, 178°18′W, 25 May 1966, 1658-1956 hrs, depth sampled 0-900 m, bottom depth 2641 m, one specimen, 66.0 mm (otolith photographed, Fig. 10).

USNS ELTANIN, cruise 26, sta. 1820, 40°22′S, 168°25′E, 2 December 1966, 2000-2319 hrs, depth sampled 0-750 m, bottom depth 920-1028 m, one specimen 109.0 mm.

R/V ANTON BRUUN, cruise III, sta. 157, 32°11′S, 59°30′E, 8 September 1963, 1510-1835 hrs, depth sampled 150-750 m, bottom depth 4389 m, four specimens, 21.0-24.0 mm.

R/V ANTON BRUUN, cruise VI, sta. 352B, 34°14′S, 64°58′E, 30 June 1964, 1420-2000 hrs, depth sampled 350-750 m, bottom depth 2700 m, two specimens, 20.0-20.5 mm.

R/V ANTON BRUUN, cruise XIII, coll. 54, 33°42′S, 73°35′W, 2 February 1966, 0320-0920 hrs, depth sampled 0-500 m, one specimen, 70.5 mm.

R/V CAP'N BILL III, sta. RHB 913, 39°26′N, 71°00′W, 13 October 1962, 1020-1505 hrs, depth sampled 0-715 m, 64′ midwater trawl, one specimen, 128.0 mm; sta. RHB 914, 39°32′N, 71°00′W, 13 October 1962, 1545-2025 hrs, depth sampled 0-715 m, 64′ midwater trawl, one specimen, 130.0 mm; sta. RHB 915, 39°36′N, 71°12′W, 13 October 1962, 2105-0025 hrs, depth sampled 0-550 m, 64′ midwater trawl, one specimen, 126.0 mm (otolith photographed, Fig. 4).

R/V ATLANTIS II, cruise 13, sta. RHB 1023, 43°16′N, 45°03′W, 10

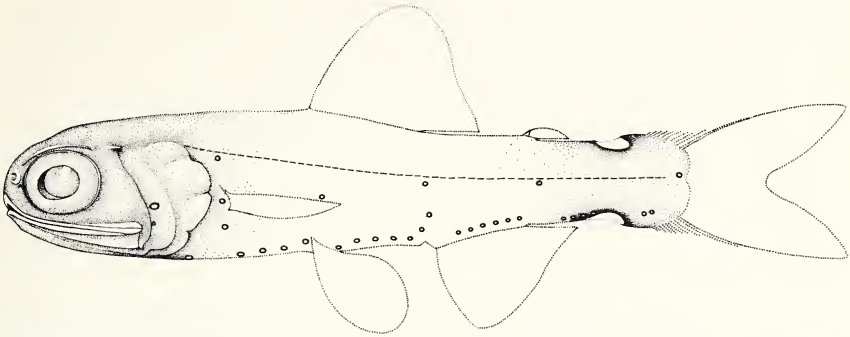

Figure 3. *Lampadena speculigera*, 66.0 mm in standard length; 41° 44′ S, 178° 18′ W.

September 1964, 0855-1230 hrs, depth sampled 0-700 m, two specimens, 33.0 mm; sta. RHB 1006, 41°16′N, 57°37′W, 4 September 1964, 1947-2330 hrs, depth sampled 0-85 m, four specimens, 29.0-36.0 mm; sta. RHB 1003, 41° 36′N, 60°30′W, 3 September 1964, 2021-2345 hrs, depth sampled 0-60 m, one specimen, 28.0 mm.

D. 14(13-15); A. 14(15); P. 14(15); V. 8; gill rakers 6-7+1+12-14, total 19-22; PO 5(6); VO 5(4-6); AOa 6-7; AOp 3-4(5); Prc 2+1; lateral line scales 39-41; vert. 38-39(40), 5 x-rayed specimens. Of 15 specimens examined, the following counts were found only once: D. 13; PO 6; VO 4; AOp 5.

Snout bluntly rounded; mouth large, barely subterminal, its cleft very slightly oblique; eye large, its diameter 2.7 to 3.2 in length of head; opercular margin not pointed, but with a shallow indentation about on level of upper end of pectoral base; pterotic spine strong, straight, directed posterolaterally.

Origin of dorsal fin on or slightly behind vertical through base of outermost ray of ventral fin; origin of anal fin behind vertical through end of base of dorsal fin; base of adipose fin over end of base of anal fin; pectoral fin extending to about level of first VO; ventral fin reaching origin of anal fin.

A small Vn, immediately posteroventrad to nasal apparatus and directed ventrally; anterior third of orbital margin lined with black tissue. $Op_1$ small, immediately behind lower preopercular margin and opposite posterior end of mouth; $Op_2$ markedly larger than general body photophores, at least one times its own diameter above level of ventral margin of orbit and about 2.5 times its own diameter above and slightly behind $Op_1$.

PLO distinctly in advance of vertical through base of uppermost ray of pectoral fin and about one photophore diameter below lateral line; $PVO_1$ somewhat above level of posterior end of maxillary, slightly behind vertical through $PVO_2$, which is situated in front of lower half of base of pectoral fin and on a straight line connecting PLO with $PVO_1$. $PO_1$-$PO_2$ interspace about

twice as wide as $PO_4$-$PO_5$ interspace, which is equal to or slightly wider than rest; $PO_1$-$PO_3$ in a horizontal line; $PO_5$ situated about its own diameter in front of, and slightly mesad to, base of outermost ray of ventral fin; $PO_4$ much closer to horizontal level of $PO_3$ than to that of $PO_5$. VLO distinctly behind vertical through base of outermost ray of ventral fin and somewhat closer to lateral line than to base of ventral fin; VO more or less level and evenly spaced, sometimes last VO slightly raised; $VO_1$ posteromesad to base of innermost ray of ventral fin. SAO forming a wide angle; $SAO_1$ above and behind last VO; $SAO_2$ above and behind $SAO_1$; $SAO_2$-$SAO_3$ interspace about 2.5 times as wide as $SAO_1$-$SAO_2$ interspace, which is equal to that of $VO_5$-$SAO_1$; $SAO_3$ slightly in advance of vertical through $SAO_2$ and its own diameter, or less, below lateral line. AO small, especially in young specimens; AOa level, evenly spaced, about one photophore diameter (one to two diameters in fishes less than 30 mm) apart from each other. Pol behind last AOa and about its own diameter below lateral line; AOp evenly spaced, on a straight, gently ascending line; $AOp_1$ and usually $AOp_2$ in front of anterior end of infracaudal luminous gland. $Prc_1$ and $Prc_2$ horizontal or $Prc_2$ slightly raised, the two photophores being only one organ diameter apart from each other; $Prc_3$ at base of middle rays of caudal fin and very slightly above level of lateral line.

Figure 4. *Lampadena speculigera*, medial view of left otolith, 4.9 mm long, 3.5 mm high, belonging to an 126 mm specimen from the north Atlantic.

Length of supracaudal gland one-half to two-thirds that of infracaudal; posterior margin of both glands at about same vertical; posterior margin of supracaudal gland distinctly emarginate; distance between posterior end of base of anal fin and anterior margin of infracaudal luminous gland 1 to 1.5 times as great as length of this gland.

Premaxillary and especially dentary with bands of small, needlelike teeth; an inner series of 10 to 15 enlarged, broad-based, recurved teeth directed anteriorly on posterior dentary; two to five large, anteriorly directed, recurved teeth on inner margin of dentary close to symphysis (more prominent in large specimens, 80 mm or more); anterior end of premaxillary broadened, forming a roughly triangular dentigerous area outside the mouth; teeth of outer row of this area enlarged, recurved, directed posteroventrally. Palatine with long, narrow band of small teeth. Few minute teeth on each distal end of vomer. Mesopterygoid with large, roughly oval, patch of uniformly small teeth.

Neural arches of anterior vertebrae greatly expanded to form an almost closed tube above vertebrae.

Two trends can be distinguished between specimens from the two hemispheres. These involve AO and gill-raker counts. Individuals from the southern oceans tend to have 6+4 AO and 7+1+13-14 gill rakers, whereas in those from the north Atlantic, 7+3 AO and 6+1+12-13 gill rakers are the most frequent counts. In addition, John Fitch called our attention to the fact that the otoliths from a specimen 126 mm long taken in the north Atlantic (Fig. 4), were distinctly different from those of specimens from the southern hemisphere (Fig. 10 (4)). Some changes in size and shape, depending on the size of the specimens and the length of time of preservation, are to be expected. However, the differences in the present case are strong enough to warrant an examination of larger material, especially from the north Atlantic. Until this is done we prefer to consider the two populations as conspecific.

Our material from the southern hemisphere indicates that *Lampadena speculigera* is a subtropical-temperate form, ranging, in the Indian and Pacific Oceans, between the latitudes of approximately 30°S and 45°S. It is considered relatively common in the north Atlantic (Bolin, 1959). On the basis of material from the collections of the Woods Hole Oceanographic Institution, this species appears to range between the latitudes of approximately 35°N and 45°N in the north Atlantic (Fig. 9). Further study of large collections is necessary before its apparent absence from the south Atlantic can be ascertained.

### **Lampadena notialis,** new species

Fig. 5

*Holotype*: LACM 11321-1; immature specimen, 66.3 mm, USNS ELTANIN, cruise 26, sta. 1830, 42°00′S, 160°11′E to 42°08′S, 160°05′E, 8

December 1966, 0839-1140 hrs, depth sampled 0-800 m, bottom depth 4895 m (otolith photographed, Fig. 10).

*Paratypes*: LACM 11331-1; a male specimen, 105.0 mm, USNS EL-TANIN, cruise 26, sta. 1841, 47°20′S, 161°54′E to 47°28′S, 161°52′E, 12-13 December 1966, 2334-0221 hrs, depth sampled 0-800 m, bottom depth 4648 m. MCZ 45892; one specimen, 25.2 mm; R/V ANTON BRUUN, cruise VI, sta. 354A, 40°48′S, 65°03′E, 4 July 1964, 0915-1510 hrs, depth sampled 0-1650 m, bottom depth 4600 m.

D. 14; A. 14; P. 14; V. 8; gill rakers 7-8+1+16-17, total 24-26; PO 5; VO 5(6); AOa 6; AOp 3; Prc 2+1; lateral line scales 38-39; vert. 37-38, 2 x-rayed specimens.

A relatively large myctophid fish; body rather robust, gently tapering from vertical through base of pectoral fin to a deep caudal peduncle; dorsal and ventral contours anterior to pectoral fin evenly curved; snout rather high and bluntly rounded; mouth large, slightly subterminal, its cleft moderately oblique; eye large, its diameter 2.8 to 3.0 in length of head; posterior opercular margin produced into two rounded lobes separated by a triangular indentation located at about level of $PVO_2$; pterotic spine directed posterolaterally in younger specimen (holotype) and posteroventrally in mature specimen (paratype).

Origin of dorsal fin distinctly in advance of vertical through base of outermost ray of ventral fin; origin of anal fin behind vertical through end of base of dorsal fin; base of adipose fin about over end of base of anal fin; rays of pectoral fin extending slightly beyond base of ventral fin; rays of ventral fin reaching first or second ray of anal fin.

Vn well developed, immediately posteroventral to nasal apparatus, roundish, directed ventrally and framed dorsally and laterally by darkly pigmented tissue; a narrow strand of black tissue along entire anterior margin of orbit,

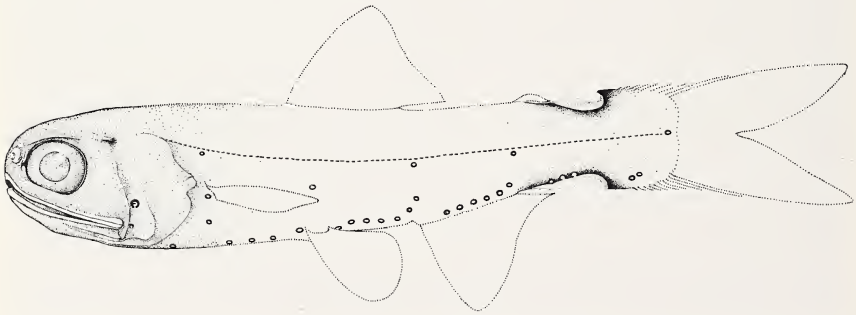

Figure 5. *Lampadena notialis*, new species, holotype, 66.3 mm in standard length; 42° 00′ S, 160° 11′ E; LACM 11321-1.

extending ventrally and posteriorly up to about vertical through center of pupil; suborbital region with numerous pores, each with a raised, darkly-pigmented ridge. $Op_1$ small, immediately behind preopercular margin and directly opposite or slightly below level of posterior end of maxillary, often masked by whitish tissue of adjacent neuromasts; $Op_2$ larger than general body photophores, at about level of ventral margin of orbit, slightly posterior to vertical through $Op_1$ and separated from latter by a distance about twice as large as its own diameter.

PLO slightly in advance of vertical through upper end of base of pectoral fin and 1.5 to 2 times its own diameter below lateral line. $PVO_1$ at about level of posterior end of mouth, directly under or slightly posterior to $PVO_2$, which is about its own diameter in front of ventral half of base of pectoral fin. PO series forming gently diverging lines; first PO interspace 2 to 2.5 times as wide as spaces between rest of organs of same series; $PO_5$ about its own diameter from, and slightly mesad to, base of outermost ray of ventral fin. VLO slightly behind vertical through base of outermost ray of ventral fin and somewhat closer to lateral line than to base of ventral fin. LACM paratype with five VO distinctly divided into two groups (2+3) on the left side and six evenly spaced VO on the right side; holotype and smaller paratype with five evenly spaced VO on both sides, the organs forming a gentle arch; $VO_1$ posteromesad to base of innermost ray of ventral fin. SAO slightly angular; $SAO_1$ about its own diameter behind and above last VO; $SAO_2$ (not developed on left side of larger paratype) about its own diameter above, but only slightly behind $SAO_1$; $SAO_3$ directly over or slightly behind $SAO_2$, its own diameter or less below lateral line and separated from $SAO_2$ by a distance 2 to 3 times as wide as that between $SAO_1$ and $SAO_2$. AOa evenly spaced, interspaces about 1.5 times the diameter of an organ of same series (less than the diameter of a photophore in fishes less than 30 mm); all but last AOa level, latter distinctly raised, its ventral margin touching tangent to dorsal border of preceding organ. Pol behind last AOa and less than its own diameter below lateral line; all three AOp on anterior, ascending dorsal contour of infracaudal luminous gland; AOp interspaces equal to one diameter of an organ of same series, or less; $Prc_1$-$Prc_2$ interspace equal to about half the diameter of an organ of same series; $Prc_2$ slightly raised; $Prc_3$ at base of middle rays of caudal fin and slightly above level of lateral line.

Supra- and infracaudal luminous glands very well developed; length of supracaudal gland about three-fourths that of infracaudal gland; length of infracaudal gland equal to (in small specimens) or greater than (in large specimens) diameter of eye; distance between posterior end of base of anal fin and anterior end of infracaudal gland equal to about one-fourth of length of that gland.

Premaxillary and dentary studded with small, villiform teeth; an inner series of eight to nine large, recurved forward, very broad-based teeth at

posterior end of dentary (particularly large in medium-sized fish—*i.e.*, size of holotype); an inner series of widely spaced, large teeth hooked forward along anterior end of dentary (best developed in large individuals); anterior dentigerous ends of premaxillaries broadened near symphysis, forming a triangular area with an outer row of enlarged teeth recurved anteroventrally. Palatine teeth very small, papilliform, arranged in a long and narrow band. A small patch of minute teeth on distal end of each limb of vomer. A large, roughly oval patch of somewhat larger teeth on each mesopterygoid.

Neural arches of anterior vertebrae not greatly expanded.

The specific name comes from the Greek *notia,* which means southern, in reference to the occurrence of the species in high southern latitudes (Fig. 8).

### **Lampadena dea** Fraser-Brunner, 1949

Fig. 6

R/V ANTON BRUUN, cruise III, sta. 156, 28°54′S, 60°01′E, 6-7 September 1963, 2155-0240 hrs, depth sampled 0-275 m, bottom depth 4114 m, one specimen, 23.0 mm; sta. 156, 29°13′S, 60°05′E, 7 September 1963, 0245-0620 hrs, depth sampled 0-150 m, bottom depth 4114 m, two specimens, 21.0 mm.

R/V ANTON BRUUN, cruise VI, sta. 352B, 34°14′S, 64°58′E, 30 June 1964, 1420-2000 hrs, depth sampled 350-750 m, bottom depth 2700 m, one specimen, 37.0 mm; sta. 353A, 37°59′S, 64°56′E, 2 July 1964, 1115-1925 hrs, depth sampled 350-2390 m, bottom depth 4400-4600 m, one specimen, 63.5 mm.

R/V ANTON BRUUN, cruise XIII, coll. 22, 33°51′S, 87°49′W, 18 January 1966, 0013-0530 hrs, depth sampled 0-375 m, bottom depth 3550-3900 m, one specimen, 45.5 mm; coll. 28, 30°45′S, 92°34′W, 22 January 1966, 0045-0650 hrs, depth sampled 0-320 m, bottom depth 3450-3710 m, two specimens, 35.0-39.5 mm; coll. 30, 31°07′S, 89°29′W, 24 January 1966, 0025-0350 hrs, depth sampled 0-410 m, bottom depth 3550-3950, two specimens, 27.0-40.0 mm.

USNS ELTANIN, cruise 24, sta. 1739, 40°15′S, 144°45′W, 26 July 1966, 0204-0530 hrs, depth sampled 0-1125 m, bottom depth 5325 m, one specimen, 59.0 mm (otolith photographed, Fig. 10).

D. 14; A. 14(15); P. 14(15); V. 8; gill rakers 6(7)+1+14(15), total 21(22-23); PO 5; VO 5(4-6); AOa 6-7(5); AOp 4-5(3); Prc 2+1; lateral line scales 37-38; vert. 38, 3 x-rayed specimens. Of ten specimens examined, the following counts occurred only once: A. 15; gill rakers 7+1+14, 7+1+15; VO 4, 6; AOp 3.

The 11 specimens in the collection yielded 22 AO counts, as follows: 5+4(4), 6+3(1), 6+4(6), 6+5(6), 7+4(4), and 7+5(1).

Snout bluntly rounded; mouth large, slightly subterminal, its cleft some-

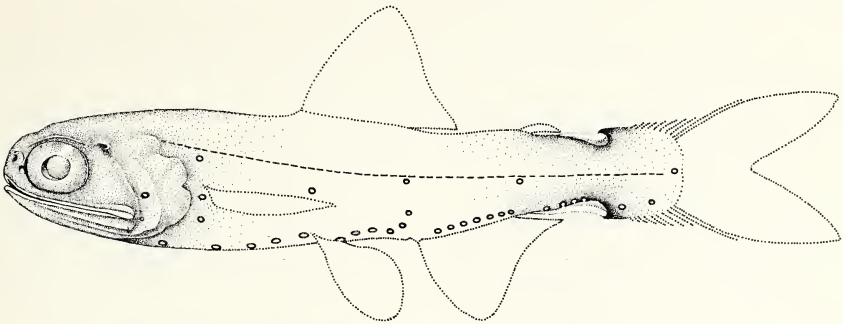

Figure 6. *Lampadena dea*, 59.0 mm in standard length; 40° 15′ S, 144° 45′ W.

what oblique; eye large, its diameter 2.9 to 3.3 in length of head; opercular margin with a very distinct triangular indentation at about level of upper half of base of pectoral fin; pterotic spine very strong, curved downward and forward in larger specimens, posterolaterally in smaller specimens.

Origin of dorsal fin over or slightly in advance of vertical through base of outermost ray of ventral fin; origin of anal fin behind vertical through end of base of dorsal fin; base of adipose fin somewhat behind vertical through end of base of anal fin; pectoral fin extending to about level of second VO; ventral fin reaching base of second or third anal ray.

Vn present, posteroventral to nasal apparatus, directed ventrally; anterior third of orbital margin lined with black tissue. A small $Op_1$, difficult to see, close to and directly behind posterior end of maxillary; $Op_2$ distinctly larger than general body photophores, about on level of ventral margin of orbit and slightly behind vertical through $Op_1$.

PLO slightly in advance of vertical through upper end of base of pectoral fin and about its own diameter below lateral line. $PVO_1$ at about level of posterior end of mouth, directly under or slightly in advance of vertical through $PVO_2$, which is found in front of middle of base of pectoral fin and slightly behind straight line connecting PLO with $PVO_1$. PO series forming posteriorly diverging lines, with $PO_5$ situated about its own diameter in front of, and slightly mesad to, base of outermost ray of ventral fin; first PO interspace about 1.5 times as wide as others; $PO_4$ closer to horizontal level of $PO_3$ than to that of $PO_5$. VLO directly over or slightly in advance of vertical through base of outermost ray of ventral fin and markedly closer to lateral line than to base of ventral fin. VO equally spaced or distinctly grouped (2+3), the entire series on a gently arched line; $VO_1$ posteromesad to base of innermost ray of ventral fin. SAO forming a wide angle; $SAO_1$ above and behind last VO; $SAO_2$ above and behind $SAO_1$; $SAO_2$-$SAO_3$ interspace 2 to 2.5 times as wide as $SAO_1$ $SAO_2$ interspace, which is equal to that of $VO_5$-$SAO_1$; $SAO_3$ directly over,

slightly anterior, or immediately posterior to $SAO_2$, and 0.5 to 1 time its own diameter below lateral line. AOa level and usually evenly spaced. Pol behind vertical through last AOa and less than one times its own diameter below lateral line. AOp evenly or irregularly spaced, but all organs over anterior two-thirds of infracaudal gland. $Prc_1$ anterior to first ventral procurrent spine; $Prc_1$ and $Prc_2$ on same horizontal level or $Prc_2$ slightly raised, the two organs separated by a distance equal to at least three photophore diameters; $Prc_3$ at base of middle rays of caudal fin, and slightly above level of lateral line.

Supra- and infracaudal luminous glands well developed; length of supracaudal gland about two-thirds length of infracaudal gland; posterior margin of both glands on same vertical; posterior margin of supracaudal gland slightly or distinctly emarginate; distance between anterior end of infracaudal gland and posterior end of base of anal fin less than one-fourth the length of infracaudal gland.

Premaxillary and dentary with a band of small, conical teeth; inner series of 6-8 large, broad-based, widely-spaced, recurved teeth directed anteriorly on posterior third of dentary; two or three larger inner teeth on anterior dentary near symphysis, but these are not recurved; anterior dentigerous portion of premaxillary near symphysis slightly widened, with curved teeth. Narrow band of small teeth on palatine. No teeth evident on vomer. Elongated oval patch of small, uniformly-sized teeth on mesopterygoid.

Neural arches of anterior vertebrae greatly expanded to form an almost closed tube above centra.

*Lampadena dea* occurs in the southern parts of all three oceans, between the latitudes of approximately 20°S and 50°S (Fig. 9).

### **Lampadena chavesi** Collett, 1905

Fig. 7

R/V ANTON BRUUN, cruise VI, sta. 351D, 31°45′S, 65°08′E, 29 June 1964, 0359-1507 hrs, depth sampled 350-1786 m, bottom depth 4480 m, one specimen, 54.5 mm.

R/V ANTON BRUUN, cruise XIII, coll. 26, 31°16′S, 92°28′W, 20-21 January 1966, 2014-0138 hrs, depth sampled 0-380 m, bottom depth 3300-3700 m, one specimen, 60.0 mm; coll. 30, 31°07′S, 89°29′W, 24 January 1966, 0025-0350 hrs, depth sampled 0-410 m, bottom depth 3550-3950 m, two specimens, 36.0-38.0 mm (otolith of 36.0 mm specimen photographed, Fig. 10).

R/V ATLANTIS II, cruise 13, sta. RHB 1014, 41°34′N, 52°15′W, 7 September 1964, 0115-0500 hrs, depth sampled 0-85 m, one specimen, 19.0 mm; sta. RHB 1022, 42°35′N, 45°56′W, 10 September 1964, 0135-0505 hrs, depth sampled 0-50 m, two specimens, 22.0-24.0 mm; sta. RHB 1044, 39°37′ N, 31°10′W, 26 September 1964, 0050-0535 hrs, depth sampled 0-475 m, one

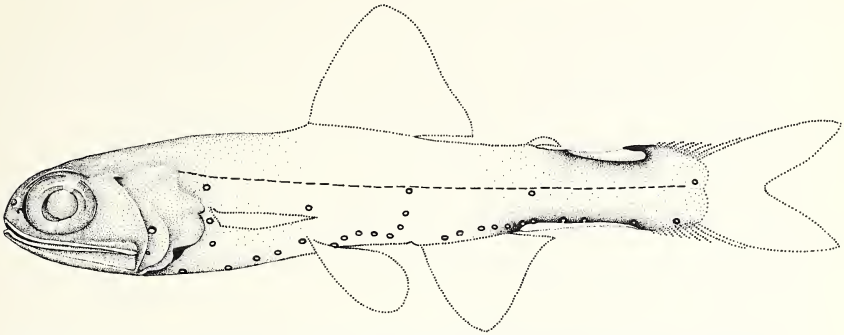

Figure 7. *Lampadena chavesi*, 54.5 mm in standard length; 31° 45′ S, 65° 08′ E.

specimen, 35.0 mm; sta. RHB 1047, 39°25′N, 36°56′W, 27 September 1964, 2030-2250 hrs, depth sampled 0-52 m, one specimen, 21.0 mm.

R/V CHAIN, cruise 49, sta. RHB 1127, 31°28′N, 70°25′W, 22 June 1965, 0035-0330 hrs, depth sampled 0-83 m, two specimens, 22.0-25.0 mm; sta. RHB 1129, 34°12′N, 70°21′W, 22 June 1965, 2145-2355 hrs, depth sampled 0-80 m, one specimen, 27.0 mm.

D. 14; A. 13-14(12); P. 16-17; V. 8; gill rakers 6-7+1+13, total 20-21; PO 5; VO 5(6); AOa 7(8); AOp 2; Prc 2+1; lateral line scales 38(39); vert. 37-38, 2 x-rayed specimens.

Snout rounded; mouth large and terminal, its cleft very slightly oblique; maxillary somewhat expanded posteriorly; eye large, its diameter 2.6 to 3.3 times in length of head; opercular margin with slight indentation opposite level of middle of pectoral base; pterotic spine strong, directed posteriorly.

Origin of dorsal fin over or slightly behind vertical through base of outermost ray of ventral fin; origin of anal fin behind vertical through end of base of dorsal fin; base of adipose fin markedly behind vertical through end of base of anal fin; pectoral fin reaching base of ventral fin; ventral fin extending to origin of anal fin.

A small, roundish Vn immediately posteroventrad to nasal apparatus; anterior third of orbital margin lined with black tissue; a conspicuous, crescent-shaped strip of whitish (luminous?) tissue on iris dorsal to pupil, which is somewhat elliptical; distinct aphakic space anteroventrad to lens. $Op_1$ small, immediately behind preopercular margin and about opposite posterior end of mouth; $Op_2$ distinctly larger than general body photophores, at about level of ventral margin of pupil, separated from $Op_1$ by a distance about three times as wide as its own diameter.

PLO slightly in advance of vertical through base of uppermost ray of pectoral fin and 1 to 1.5 times its own diameter below lateral line. $PVO_1$ at about level of posterior end of mouth, slightly posterior to vertical through

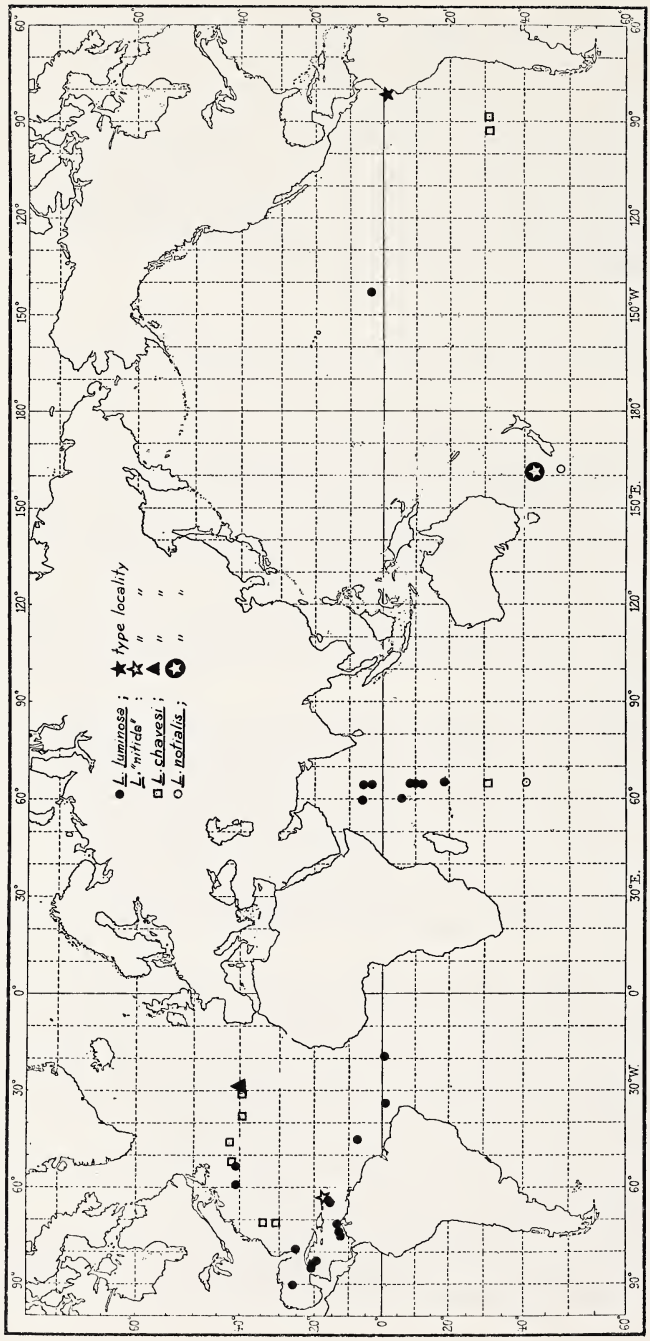


Figure 8. Chart showing stations which yielded material examined in the present study (the type locality of *L. chavesi* was added from the literature).

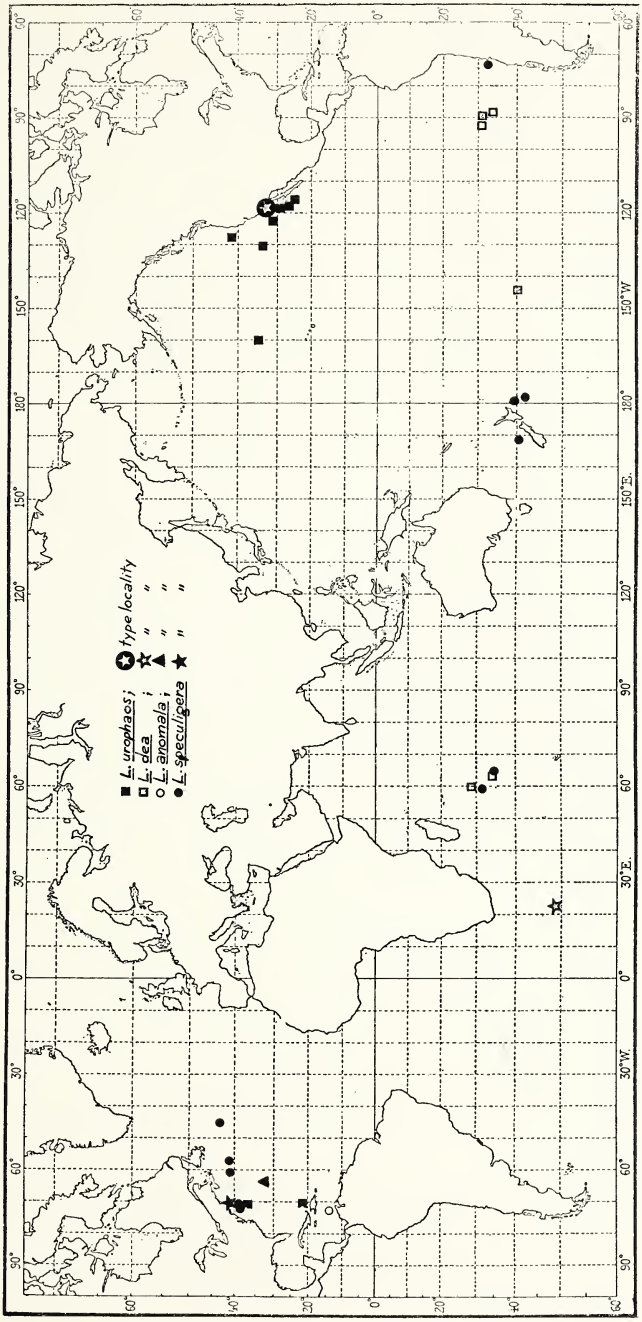


Figure 9. Chart showing stations which yielded material examined in the present study (the type localities of *L. dea* and *L. speculigera* were added from the literature).

$PVO_2$, which is situated in front of middle of base of pectoral fin and on a straight line connecting PLO with $PVO_1$. $PO_1$ and $PO_2$ on a straight, horizontal line; $PO_2$ through $PO_5$ in straight, diverging lines, with $PO_5$ situated about 1.5 times its own diameter in front of and slightly mesad to base of outermost ray of ventral fin; first PO interspace 1.5 to 2 times as wide as last, which is somewhat wider than $PO_2$-$PO_3$ and $PO_3$-$PO_4$ interspaces; VLO over base of outermost ray of ventral fin and midway between latter and lateral line. VO evenly spaced or distinctly grouped (2+3) forming a markedly arched line; $VO_1$ directly mesad, or slightly anterior, to base of innermost ray of ventral fin. SAO series very slightly angular; $SAO_1$ above and behind $VO_5$; $SAO_2$ above and behind $SAO_1$; $SAO_3$ directly over, slightly anterior, or immediately posterior to vertical through center of $SAO_2$ and about its own diameter below lateral line; distance between $SAO_3$ and $SAO_2$ about twice as wide as distance between $SAO_2$ and $SAO_1$, the latter being equal to that between $SAO_1$ and $VO_5$. First and second AOa somewhat depressed; space between $AOa_2$ and $AOa_3$ usually distinctly wider than other AOa interspaces; last two to three AOa entirely behind base of anal fin; at least one and usually two AOa over infracaudal luminous gland. Pol over or slightly posterior to last AOa and about its own diameter below lateral line. AOp widely spaced, about over middle of, and in contact with, infracaudal gland. $Prc_1$ over posterior end of infracaudal gland; $Prc_1$ and $Prc_2$ horizontally arranged and very widely spaced, distance between them equal to, or somewhat smaller than, distance between $Prc_2$ and $Prc_3$, which is posterior to $Prc_2$ and slightly above level of lateral line.

Caudal luminous gland largest in genus, their posterior borders on same vertical; supracaudal gland bifurcating posteriorly; infracaudal gland flat in cross section, limited to ventral area of caudal peduncle and not conspicuous laterally, tapering posteriorly rather than anteriorly (in contrast to all other species of the genus); distance between end of base of anal fin and anterior margin of infracaudal gland very short, about twice the diameter of a photophore.

Premaxillary and dentary with band of small, needlelike teeth; six to eight large, recurved, broad-based teeth directed anteriorly on posterior part of dentary; three to four inner, moderately large teeth hooked forward on anterior portion of dentary near symphysis; premaxillary slightly broadened near symphysis, with outer row of large, recurved teeth. Palatine with long, narrow band of minute teeth. A small patch of minute teeth on each limb of vomer. Large, oval patch of similar teeth on mesopterygoid.

Neural arches of anterior vertebrae greatly expanded to form an almost closed tube above centra.

Bolin (1959) states that "*Lampadena chavesi* appears to occur throughout the Atlantic between the latitudes of approximately 38°N and 33°S." Our data suggest that this species occurs in the North Atlantic between the latitudes of about 30°N and 45°N and in both the Indian and Pacific Oceans between

the latitudes of approximately 30°S and 40°S (Fig. 8). An antitropical distribution is indicated.

### **Lampadena anomala** Parr, 1928

R/V PAWNEE, sta. 58B, 32°24′N, 64°29′W, 20 March 1927, depth sampled 0-ca. 2000 m, 14-foot Ring Net, one specimen (holotype), ca. 48 mm, BOC 2272.

R/V CHAIN, cruise 60, sta. RHB 1260, 13°12′N, 72°47′W, 28 May 1966, 1050-1400 hrs, depth sampled 0-890 m, Marinovich Trawl, one specimen, about 48 mm (otolith photographed, Fig. 10).

Parr (1928) described this species on the basis of a single 48 mm specimen. Because of the poor condition of the fish, Parr was unable to take accurate measurements. Unfortunately, the only specimen from the Woods Hole collection is in equally poor, if not poorer, condition. However, direct comparison with Parr's type left us with no doubt that it belongs to *L. anomala.* The following description is based on the characters which we have been able to positively locate, identify, and count in the Woods Hole specimen.

D. 16; A. 13; P. 16; V. 8; gill rakers 5+1+11; VO 3; SAO 3; AOa 3 on left side, 4 on right; AOp 2; Prc 2+1; vert. 36.

Photophores small, more so than in any other species of the genus; two Op (Parr's ". . . a series of six small organs . . .", mistaken for photophores, are nothing but a series of neuromasts immediately behind the preopercular margin, found in all myctophids); PLO in advance of vertical through upper end of base of pectoral fin, about twice its own diameter below lateral line. $PVO_1$ slightly behind vertical through center of $PVO_2$, which is immediately in front of middle of base of pectoral fin. VLO slightly nearer lateral line than base of ventral fin; three VO widely spaced. $SAO_3$ about over origin of anal fin and about its own diameter below lateral line. AOa level, widely spaced; last AOa well in advance of end of base of anal fin. Pol behind end of base of anal fin, about twice its own diameter below lateral line. $AOp_1$ in advance of anterior margin of infracaudal luminous gland; $AOp_2$ over same gland; $AOp_1$-$AOp_2$ interspace about twice the diameter of an organ; $Prc_1$ and $Prc_2$ horizontal and about one organ diameter apart from each other; $Prc_3$ near base of middle rays of caudal fin and slightly above level of lateral line.

Supracaudal luminous gland slightly shorter than infracaudal, the length of the latter being equal to distance between end of base of anal fin and anterior margin of infracaudal gland.

Premaxillary and dentary with band of small, needlelike teeth, the inner series distinctly enlarged; five broad-based, strongly recurved teeth directed anteriorly on posterior part of dentary; no evidence of enlarged teeth on anterior part of dentary or premaxillary near symphysis. Palatine with what appears to be a single, long row of relatively large, sharp teeth. One or two

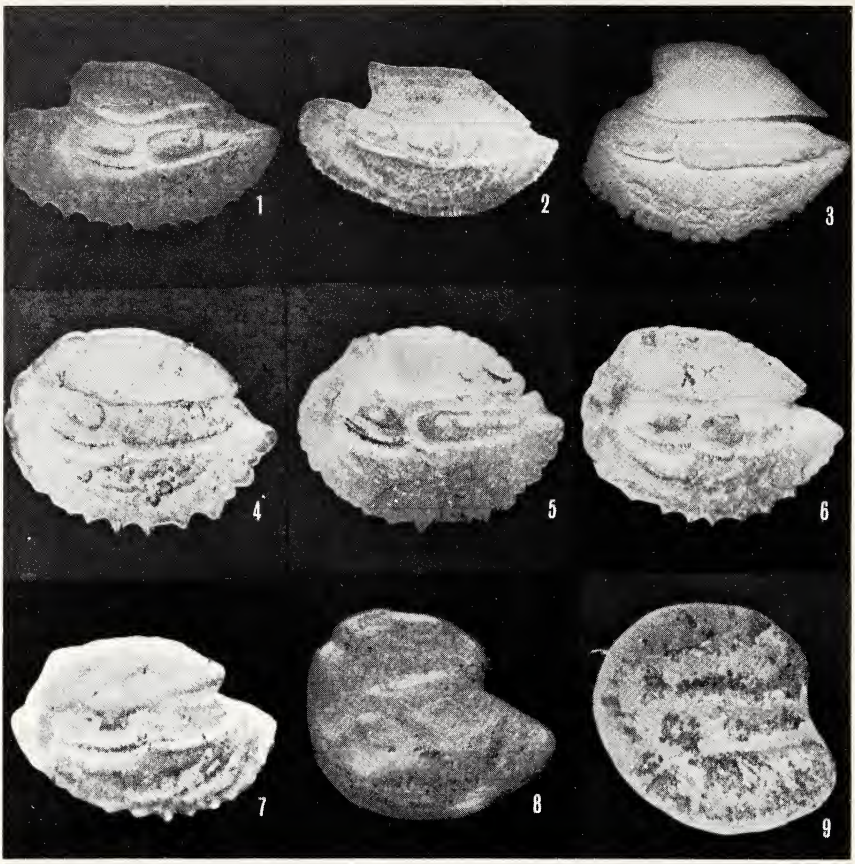


Figure 10. Medial views of left otoliths, anterior end to the right. (1) *Lampadena luminosa,* otolith 5.4 mm long, specimen 71 mm; (2) *L. urophaos,* otolith 7.6 mm long, specimen probably about 80 mm; (3) *L.* species A, otolith 9.2 mm long; (4) *L. speculigera,* otolith 3.8 mm long, specimen 66 mm; (5) *L. notialis,* otolith 3.9 mm long, specimen 66.3 mm; (6) *L. dea,* otolith 3.4 mm long, specimen 59 mm; (7) *L. chavesi,* otolith 1.7 mm long, specimen 36 mm; (8) *L. anomala,* otolith 1.8 mm long, specimen about 48 mm; (9) *Taaningichthys bathyphilus,* otolith 1.9 mm long, specimen probably about 50 mm.

teeth at each distal end of vomer. A large, roughly oval-shaped patch of similar teeth on mesopterygoid, with posterior ones somewhat enlarged.

Neural arches of anterior vertebrae not greatly expanded.

Inadequate data preclude any statement concerning the horizontal distribution of *L. anomala* (Fig. 9). However, this fish appears to occur at greater depths than the rest of its congeners.

## OTOLITHS

Sagittae of the species of the genus *Lampadena* display three main patterns (Fig. 10). *L. luminosa* and *L. urophaos* have large otoliths, considerably longer than high, with a length to height ratio of 1.7:1 to 1.8:1. The posterodorsal angle is conspicuously notched and the ventral margin is not smooth. A distinct rostrum and small antirostrum are present. The lateral face is slightly rounded and weakly sculptured. The posterior angle of the dorsal margin is pronounced (broken off in the photographed specimen of *L. luminosa*). The ventral margin of *L. urophaos* is scalloped or finely serrate, while that of *L. luminosa* has more distinct spinous processes. The collum divides the sulcus into two unequal sections in *L. urophaos,* whereas the collum is about in the middle of the sulcus in *L. luminosa. L. speculigera, L. notialis, L. dea* and *L. chavesi* have more oval-shaped otoliths, with length to height ratios varying between 1.3:1 and 1.5:1. The posterodorsal notch is slight or absent, the collum is about in the middle of the sulcus, the ventral margin has small but distinct spines, and the lateral face is slightly rounded and weakly sculptured. A distinct rostrum and antirostrum are present in *L. dea* and *L. chavesi,* while these structures are less conspicuous in *L. speculigera* and *L. notialis.* The posterodorsal angle is slightly indented in *L. chavesi* and essentially unnotched in the other three species. The anterior region of the dorsal margin is distinctly scalloped in *L. notialis,* while that of *L. speculigera* is almost smooth. *L. anomala* has a small otolith with a length to height ratio of 1.2:1, no posterodorsal notch, a smooth ventral margin, a greatly developed rostrum, and a distinctly rounded lateral surface. The otolith of *Taaningichthys bathyphilus* is small and nearly round, with a length to height ratio of 1.0:1, no posterodorsal notch, a smooth ventral margin, a slight to moderate rostrum, and a rounded lateral surface. Although otoliths from fishes of comparable sizes were not available, a difference in relative sizes is suggested. The ratios of standard length of specimen to otolith length are as follows: *L. luminosa*—13.1:1; *L. notialis*—16.9:1; *L. speculigera* and *L. dea*—17.4:1; *L. chavesi*—20.6:1; *L. anomala*—26.7:1. Standard lengths for the other species are not available; however, *L. urophaos*, like *L. luminosa*, has a large otolith, whereas *Taaningichthys bathyphilus*, like *L. chavesi*, has a small one.

## DISCUSSION

Fraser-Brunner (1949) erected the subgenus *Lychnophora* to include the forms *L. luminosa* and *L. nitida.* The distinguishing characters of the subgenus were given as follows: $PO_3$ ($=PO_4$) much elevated (versus PO all on same level); diameter of eye more than four times in length of head (versus eye diameter less than four times in head); and inner row of pterygoid teeth conspicuously enlarged (versus pterygoid teeth uniformly small). The present study has revealed that the latter two characters are not diagnostic for the

TABLE 1

Measurements as per cent of standard length for the species of *Lampadena*.

| | specimens | standard length | eye diam. | caud. ped. length | caud. ped. depth | preanal | infc. gland | supc. gland |
|---|---|---|---|---|---|---|---|---|
| *L. luminosa* | 10 | 22.0-151.0 | 7.3- 9.4 | 19.8-22.9 | 9.5-10.7 | 64.3-68.0 | 6.6- 9.4 | 7.0- 9.4 |
| *L. urophaos* | 9 | 19.0- 79.1 | 8.0- 9.3 | 21.3-24.3 | 8.8-11.6 | 63.3-66.6 | 6.3- 8.7 | 6.0-11.2 |
| *L. dea* | 4 | 22.8- 63.3 | 10.1-10.6 | 25.4-25.8 | 11.5-12.2 | 60.4-61.6 | 13.2-15.4 | 8.6-10.2 |
| *L. speculigera* | 4 | 23.8-109.2 | 10.4-10.9 | 22.7-24.4 | 11.2-12.9 | 63.0-63.6 | 7.3-10.1 | 5.0- 5.8 |
| *L. notialis* | 3 | 25.2-105.0 | 10.5-11.5 | 24.0-24.2 | 13.8-14.3 | 62.6-63.9 | 11.1-12.8 | 7.5- 9.8 |
| *L. chavesi* | 5 | 34.0- 60.0 | 8.8-11.3 | 25.8-27.9 | 9.5-11.5 | 58.0-60.9 | 15.1-18.6 | about 11 |

subgenus. The eye diameter in head length for *L. luminosa* varies from 3.7 to 4.3 times, for *L. urophaos* from 3.5 to 4.1 times, and for the other species from 2.6 to 3.3 times. The most posterior mesopterygoid teeth are enlarged in *L. urophaos* and slightly enlarged in *L. anomala.* The subgenus can be defined on the basis of one character only, the elevated $PO_4$.

Since *L. nitida* is herein considered conspecific with *L. luminosa,* the subgenus is restricted to one form; its retention suggests that *L. luminosa* stands apart from its congeners. However, *L. urophaos* shares a number of characters with *L. luminosa.* In addition to the two characters noted above, each of these species has a very low gill-raker count, total 13-16, versus 17-26 for the other species, and a distinct similarity in the shape and size of the otolith. Moreover, in *L. urophaos,* the $PO_4$, although not as highly elevated as that of *L. luminosa,* is more elevated than the $PO_4$ of the rest of the species. *L. chavesi,* with extremely long caudal glands, white tissue (possibly luminous) on the iris, and the $VO_1$ in advance of or directly mesad to the base of the innermost ray of the ventral fin, stands as far from, if not further from, the main *Lampadena* stock as *L. luminosa. L. anomala,* as indicated by its otolith size and shape, development and pattern of photophores, etc., appears to be evolving in a different line. At our present state of knowledge, the degree of relationship between the various species of *Lampadena* is not clear and the retention of Fraser-Brunner's subgenera and/or the erection of new ones is, in our opinion, of little value in elucidating evolutionary trends within the genus. Therefore, we do not recognize the subgenus *Lychnophora.*

A tentative interpretation of species relationships is nevertheless possible. *L. luminosa* and *L. urophaos* are clearly related. The relatively low gill-raker count, total 17, and the absence of expanded anterior neural arches in *L. anomala* may indicate derivation from a stock ancestral to these two species. *L. speculigera* has more characters in common with *L. notialis* than with any other species, while *L. dea* appears to be intermediate between the latter two species and *L. chavesi. L. speculigera, L. dea,* and *L. chavesi* share with the genus *Taaningichthys* the expanded neural arches of the anterior vertebrae. The presence of white tissue on the iris and the restriction of the infracaudal gland to the ventral portion of the caudal peduncle suggest a possible relationship between *L. chavesi* and *Taaningichthys.* Certain measurements (Table 1) will distinguish some of the species. Allometric growth is common for most structures, including the caudal glands.

Knowledge of the biology of most lanternfishes in general, and *Lampadena* in particular, is meager. Many species of the genus are relatively large; specimens of *L. speculigera, L. notialis,* and *L. luminosa* attain a standard length of over 100 mm. Most species appear to be among the deepest-dwelling of myctophids; the two known captures of *L. anomala* with open nets have been made below 750 meters. Shallow captures of large specimens during the night, indicative of extensive vertical migration, are known only for *L. lumi-*

*nosa* and *L. urophaos*. Small (20-35 mm) specimens of *L. speculigera, L. dea,* and *L. chavesi* have been taken during the night in the upper 200 meters.

After the manuscript was completed, John Fitch brought to our attention a large series of otoliths recovered in good condition from the stomach contents of a pygmy sperm whale (*Kogia simus*) caught off Taiji, Japan. These otoliths (Fig. 10(3)) belong to a species of the genus *Lampadena*. The new otoliths are large, with posterodorsal angle distinctly notched, ventral margin sculptured, a distinct rostrum and antirostrum, a posteriorly divided sulcus, and with a slightly rounded lateral face. Distinctive differences between these otoliths and those most similar to them, *i.e. L. luminosa* and *L. urophaos,* include stronger development of the antirostrum, strong sculpturing of the lateral face, reduction of the area posterior to the sulcus, and a length to height ratio of 1.3:1 to 1.4:1. We have little doubt that the new otoliths belong to a form as yet undescribed. Moreover, we are inclined to believe that this new form, when caught, will prove to be more closely related to *L. urophaos* and *L. luminosa* than to any other species. If we may venture a further prediction, the new species will probably have a small number of gill rakers, unexpanded anterior neural arches, and short caudal luminous glands.

## ACKNOWLEDGMENTS

We wish to thank our colleagues of the University of Southern California who, on board the USNS ELTANIN and the USC research vessel VELERO IV, helped collect material for the present study. We also wish to thank Giles W. Mead of the Museum of Comparative Zoology (MCZ), Harvard University, for allowing us to examine the type specimen of *Lampadena luminosa* and to study material collected by the R/V ANTON BRUUN during the International Indian Ocean Expedition. Erik Bertelsen, of the Danish Marine Biological Laboratory, Carlsberg Foundation, and Keith S. Thomson, of Peabody Museum, Yale University (BOC), kindly placed the types of *L. nitida* and *L. anomala,* respectively, at our disposal. Thanks to Richard H. Backus (RHB) and James E. Craddock of the Woods Hole Oceanographic Institution, Richard H. Rosenblatt and Robert L. Wisner of the Scripps Institution of Oceanography (SIO), and Robert J. Lavenberg of the Los Angeles County Museum of Natural History (LACM), we were able to examine and compare material from the north Atlantic and the north Pacific. We are indebted to Rolf L. Bolin for having made available to us his personal file containing meticulous notes and careful descriptions of type material examined by him in various museums and collections around the world. We thank John E. Fitch and Jack W. Schott of California Fish and Game for taking the otolith photographs. Robert L. Brownell kindly provided the identification and locality of the pigmy sperm whale. Professor Bolin and Robert Lavenberg have generously given of their time to read and criticize the present work.

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# A NEW GENUS OF MUSTELID FROM THE ELLENSBURG FORMATION, WASHINGTON

*By* LAURIE J. BRYANT

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DOROTHY M. HALMOS
*Editor*

# A NEW GENUS OF MUSTELID FROM THE ELLENSBURG FORMATION, WASHINGTON

*By* LAURIE J. BRYANT[1]

ABSTRACT: *Beckia grangerensis,* n. gen. and sp., is the second reported genus of mellivorine mustelids from the Pliocene of North America. Probably representative of an Asian emigrant, the type specimen was found in association with remains of other late Clarendonian animals, including horse and camel. The jaw is that of an animal about the size of a modern wolverine, showing similarities to both *Mellivora* and *Eomellivora.*

## INTRODUCTION

American mellivorine mustelids have previously been known only from one specimen found in Pliocene deposits. A fragmentary palate of *Eomellivora* cf. *wimani* was recorded by Stock and Hall (1933) from the Hemphillian Kern River beds in Southern California. *Beckia grangerensis,* n. gen. and sp., described in this paper, is the second reported specimen of an American mellivorine. Presumably, both *Eomellivora* and *Beckia* were emigrants from Asia, where mellivorines are well known, which may have crossed the Bering land bridge and moved south down the Pacific coast.

The specimen described below was collected in Yakima County, Washington, and donated to the Los Angeles County Museum of Natural History by Mr. George F. Beck of Yakima in 1963, as part of a larger collection from the Ellensburg Formation.

The names of institutions to which specimens referred to in this paper belong, are abbreviated as follows: GSI, Geological Survey of India; LACM, Los Angeles County Museum of Natural History; SAMD, Science and Art Museum, Dublin, Ireland. Specimens belonging to the Geological Survey of India and to the Science and Art Museum, Dublin, have previously been reported and figured. Their descriptions and measurements are taken from the original citations.

## ACKNOWLEDGMENTS

Acknowledgment is made to Theodore Downs and J. R. Macdonald, who read and criticized the manuscript, and to Mrs. E. Templeton, who drew the figures.

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MUSTELIDAE Swainson, 1835
MELLIVORINAE Gill, 1872
**Beckia,** new genus

*Genotypic Species*: *Beckia grangerensis,* new species

*Geologic Range*: ? Clarendonian

*Diagnosis*: Jaw shallow, symphysis gently sloped. $M_1$ with protoconid one-third taller than paraconid; bladelike hypoconid, separated from protoconid by deep, narrow, open notch. Suggestion of metaconid on posterior blade of protoconid. Premolars elongate oblongs. $P_3$ lacking accessory cusps. Mental foramina below anterior and posterior roots of $P_3$. Tooth row straight.

**Beckia grangerensis,** new species
Figs. 1, 2

*Type*: LACM 10642, a right ramus with $P_3$-$M_1$, roots of canine and $P_2$.

*Type Locality*: LACM 6431, Granger Clay Pit, Yakima County, Washington.

*Horizon*: Ellensburg Formation, ? Clarendonian.

*Diagnosis*: As for the genus.

*Description*: $M_1$ with hypoconid only remaining cusp of the talonid; suggestion of metaconid on posterior blade of protoconid; slight cingulum around hypoconid. $M_1$ and $P_4$ overlap. $P_4$ trenchant, with slight cingulum; posterior accessory cusp small, forming part of posterior blade of principal cusp; anterior cusp very small, lying at base of principal cusp; minute anterior cingular cusp. $P_3$ crowded against $P_4$; trenchant, without anterior or posterior accessory cusps; faint anterior cingular cusp. Both premolars oblong in outline, tapered at the anterior end. $P_2$ represented by roots and fragment of base; crowded against lingual side of $P_3$.

*Comparison with Other Species of Mellivorinae*: Mellivorines are represented in the Pliocene of Asia and North America by five species in two genera; *Mellivora punjabiensis* Lydekker, *M. sivalensis* (Falconer), *Eomellivora necrophila* Pilgrim, and *E. tenebrarum* Pilgrim, all from the Siwalik Hills of India, and *E. wimani* Zdansky from Shansi and Honan provinces, China. The only previously reported mellivorine from North America is a fragmentary palate and isolated teeth from the Hemphillian Kern River beds in California which has been identified (Stock and Hall, 1933, p. 63) as *Eomellivora* cf. *wimani.* Unfortunately, *E. necrophila* and *E. tenebrarum* are known only from fragmentary specimens, and their status is questionable.

The jaw of *Beckia grangerensis* is shallower than in *Eomellivora,* the angle of the symphysis is less steep, and the premolars are more elongate than triangular. The $M_1$ is as compressed as in *E. wimani.* The premolars are taller and more trenchant. The strong cingula seen in *E. wimani* are lacking in *Beckia grangerensis.*

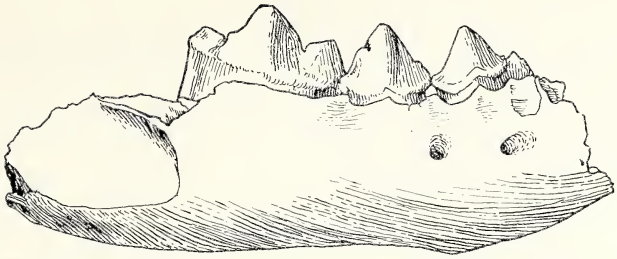

Figure 1. *Beckia grangerensis*, n. gen. and sp., LACM 10642. Right ramus with $P_3$ to $M_1$; labial view. (x 1)

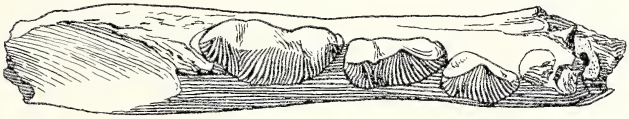

Figure 2. *Beckia grangerensis*, n. gen. and sp., LACM 10642. Right ramus with $P_3$ to $M_1$; occlusal view. (x 1)

The tooth row forms a straight line, as in *Eomellivora*; in *Mellivora sivalensis*, the tooth row is convex outward. The $P_2$ apparently was set at an angle to the other teeth, the anterior end pointing outward and the posterior end overlapping the antero-lingual corner of $P_3$. This condition is also present, and more pronounced, in *Eomellivora wimani* and *Mellivora sivalensis*.

*Geology and Associated Fauna of the Locality*: The Granger Clay Pit is presently a source of clay used in making brick. In late Clarendonian times, it may have been a pond bottom or lake area where animals were trapped in the mud or died of natural causes. The clay lens is contained in the upper or Naches Member of the Ellensburg Formation (Russell, 1900), above the Wenas Basalt (Beck, pers. comm.; Macdonald, field notes, 1965). Associated with *Beckia grangerensis* are a large tortoise, a gomphothere, *Hipparion ?anthonyi*, *?Pliauchenia* sp., a medium and a large sized camel, and an antilocaprid.

It is difficult to determine the age of the clay pit deposit. Smiley, in his study of the flora of the Ellensburg Formation (1963, p. 206), states that "Vertebrate evidence indicates an Upper Miocene (Barstovian) to Lower Pliocene (Clarendonian) age for the entire formation." From the study of the large collection made by Mr. Beck, it appears that the vertebrates indicate an age ranging from Clarendonian to Hemphillian. None seems to indicate a

Barstovian age. Even localities near the base of the formation yield assemblages including such Pliocene genera as *Hipparion* and *Nannippus*. Several *Pliohippus* teeth found near the top of the formation indicate a Hemphillian or younger age (Shotwell, 1961, p. 207).

This genus is named for Mr. George F. Beck of Yakima, Washington, who donated the specimen to the museum.

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TABLE 1

COMPARISON OF SELECTED CHARACTERS OF MELLIVORINES*

| | *Beckia grangerensis* | *Eomellivora winani* | *Eomellivora necrophila* | *Mellivora punjabiensis* | *Mellivora sivalensis* |
|---|---|---|---|---|---|
| Depth of jaw | shallow | deep | deep | shallow | not known |
| Angle of symphysis | low | steep | steep | low | not known |
| Mental foramina | below roots of $P_3$ | below post. of $P_2$, ant. of $P_4$ | not known | below ant. ends of $P_3$ and $P_4$ | not known |
| Shape of tooth row | straight | straight | straight | nearly straight | convex outward |
| Shape of premolars | elongate oblong | broad triangle | elongate oblong | $P_4$ oblong, $P_3$ elongate | broad oblong |
| Relative size of $P_3$ to $P_4$ | smaller | much smaller | slightly smaller | smaller | slightly smaller |
| Position of $P_2$ | anterior end labiad | anterior end labiad | straight; $P_3$ has anterior end linguad | straight | anterior end labiad |
| Accessory cusps | not prominent | prominent | prominent | not prominent | not known |
| Relative height of protoconid | 1/3 taller than paraconid | 1/4 taller than paraconid | 1/2 taller than paraconid | not known | not known |
| Width: length of $M_1$ | 1:2.5 | 1:2.6 | 1:3 | not known | ca. 1:2 |
| Cingula of $M_1$ | slight | strong | strong | strong | slight |

*So little material of *Eomellivora tenebrarum* is known that it is impossible to include it in this table.

TABLE 2

Measurements (in millimeters) of the jaw and lower teeth of *Beckia grangerensis* and related genera

| | *B. grangerensis* LACM 10642 Type | ***E. winnani* Type | Δ*E. necrophila** GSI D256b | Δ*E. necrophila** GSI D255b | Δ*E. necrophila** GSI D254 | Δ*E. necrophila** GSI D243 Type | +*E. tenebrarum* GSI D22 Type | +*M. punjabiensis* GSI D20 Type | +*M. sivalensis* SAMD 45 Type |
|---|---|---|---|---|---|---|---|---|---|
| $P_3$ antero-posterior diameter | 10.1 | 11.8 | | 13.3 | | | | 6.35 | 8.1 |
| transverse diameter | 6.0 | 8.3 | | 7.9 | | | | | |
| $P_4$ antero-posterior diameter | 12.9 | 15.4 | 15.5 | | | | | 9.1 | 9.65 |
| transverse diameter | 6.34 | 8.8 | 8.0 | | | | | | |
| $M_1$ antero-posterior diameter | 19.4 | 24.5 | | | | 20.4 | 22.8 | 14.2 | 13.4 |
| transverse diameter | 8.3 | 9.1 | | | | 7.7 | | | |
| depth of jaw below $M_1$ | 19.65 | 37.3* | | | 28.1 | | 25.4 | 19.8 | 17.0 |

*Measurements taken from the figure
**After Zdansky, 1924
ΔAfter Pilgrim, 1932, pl. 3, figs. 4-7
+After Lydekker, 1884

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# A NEW PLETHODONTID SALAMANDER FROM SONORA, MEXICO

*By* CHARLES H. LOWE, CLYDE J. JONES, AND JOHN W. WRIGHT

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DOROTHY M. HALMOS
*Editor*

# A NEW PLETHODONTID SALAMANDER FROM SONORA, MEXICO

*By* Charles H. Lowe[1], Clyde J. Jones[2], and John W. Wright[3]

Abstract: Recent discovery of a population of plethodontid salamanders in the Sierra Madre Occidental of extreme northwestern Mexico (Sonora) is reported. The population is described as a subspecies of *Pseudoeurycea belli*. Remarks on systematics, ecology, and biogeography are included.

A series of plethodontid salamanders were recently collected in the Sierra Madre Occidental, in southeastern Sonora, Mexico, by two field parties (see Remarks concerning itinerary and logistics) and represent the first plethodontid salamanders from northwestern Mexico. We consider them as representing a distinctive, undescribed northern subspecies of *Pseudoeurycea belli* Gray, and therefore propose:

**Pseudoeurycea belli sierraoccidentalis** subsp. nov.

Fig. 1

*Holotype*: University of Arizona, Department of Zoology (UAZ) No. 12138; Field No. CJJ 3654. Collected at *ca.* 11 mi (rd) E Santa Ana, on old road to Yécora (*ca.* 0.5 mi W Rancho El Puerto), Sonora, Mexico, by Clyde J. Jones, Charles H. Lowe, and John W. Wright, September 7, 1964. We estimate the locality to be 21 ± 1 km WSW Yécora, by old road to Nuri.

*Paratypes*: UAZ 12139-12141, 12143, LACM 39200-01, all topoparatypes.

*Diagnosis*: Distinguished most readily from other populations of *Pseudoeurycea belli* by a color pattern of a few (minimum, five) red spots of unequal size and shape scattered on the upper black body surfaces, occasionally coalesced along midline, and sometimes bilaterally paired; occipital blotches absent (Figs. 1 and 2); feet with moderately developed webbing between toes, and with the web-free toe length conspicuously short (Fig. 3).

*Description of Holotype* (*measurements in millimeters*): Adult male, prepared in field on capture (fixed in formalin, now in alcohol). Hedonic gland on chin pronounced, 7.0 wide, 4.8 long (on ventral midline). Gular fold aberrant—not a single fold in a smooth transverse line.

Snout-vent length (to posterior end of vent), 86; tail with prominent basal constriction; tail length, 68; tail width (greatest diameter at base, the tail

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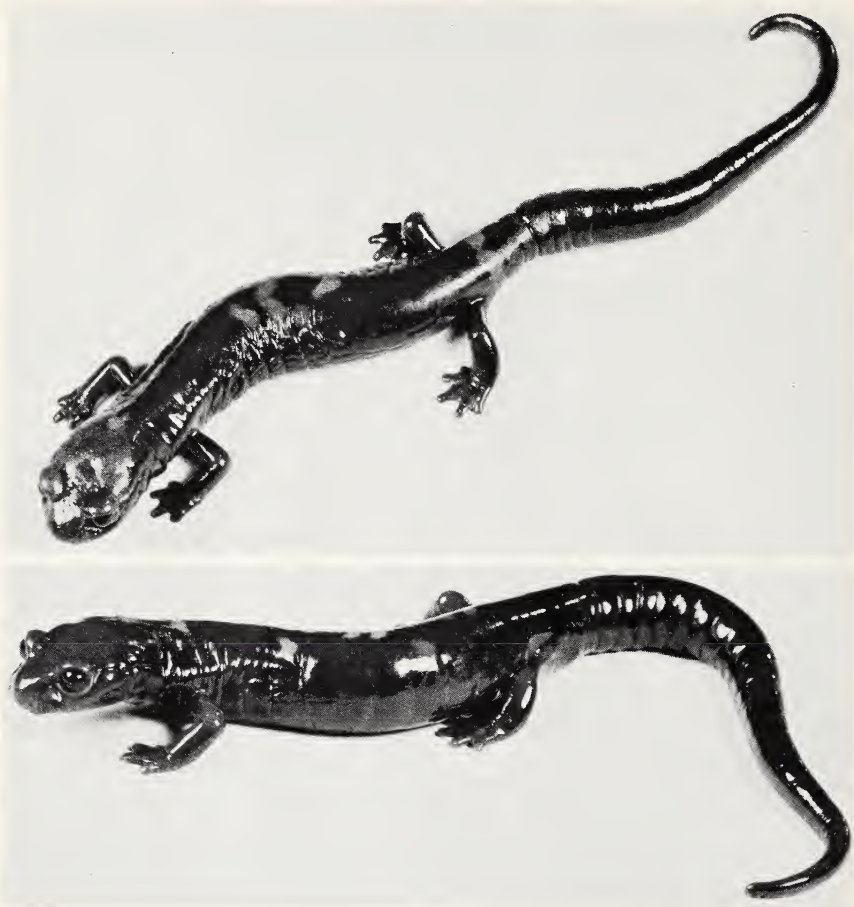

Figure 1. *Pseudoeurycea belli sierraoccidentalis* from the type locality, Sonora, Mexico. Above, adult female (UAZ 12143); below, adult male (LACM 39201).

intact), 9.1; foreleg, 19; hindleg, 19; width of foot, 7.2; snout-foreleg, 25; eye (anterior to posterior corner of lower eyelid), 5.0; head length (snout-gular fold), 19; head width, 14.5; snout-anterior corner of eyelid, 5.7; width between nostrils, 5.2; minimum interorbital distance, 3.9. Costal folds 13, counting one each in axilla and groin, three between adpressed limbs. Moderately developed webbing between toes and fingers; ascending order of size of toes, 1, 5, 2, 4, 3; of fingers, 1, 4, 2, 3. Vomerine teeth in two strongly arched (posteriorly) series, not contacting medially and extended mesially beyond choanae. Parasphenoid ("paravomerine") teeth in two contiguous groups separated anteriorly from the vomerine ("prevomerine") series.

Length of head 22.1 per cent of snout-vent length. Equivalent head length into snout-vent length, 4.53 times; this value is higher than for all other specimens in the series, due to the aberrant gular fold involved in the measurement (see *Variation*, below); head width into snout-vent length, 5.93 times.

Colors in life, black above and black to blackish below, with 12 dark red dorsal spots. Distribution of the red spots is as follows (Fig. 2): seven on the body between front and hind limb insertions, two on the body posterior to the hindlegs, two on the neck, and one on the midline across the juncture between neck and head. None of the spots are paired bilaterally on costal folds. There are neither occipital blotches, enlarged or otherwise, nor spotting on the head other than the single small midline spot across the transverse neck-line. The greatest diameter for the three largest spots of the seven on the body between axilla and groin are 3.7, 3.7, 4.2; each of these three spots is positioned obliquely, lies to the right of the midline, and is centered more or less on a costal fold (Fig. 2).

*Variation*: The series consists of seven specimens: four large adults with snout-vent lengths (mm) of 92 (♀), 88 (♀), 86 (♂), and 80 (♂); an apparent subadult (S-V L, 64 mm); and two smaller immature individuals (S-V L, 49 and 50 mm).

The number of dorsal red spots differs for each of the seven individuals. The variation, nevertheless, is within a pattern of a basic bilateral arrangement associated with the costal folds, typical of the species *P. belli* (Fig. 2). The number of red spots varies from eight to thirteen (8, 10, 12, 13; mean 10.8) in the four adults. The total number of red spots for the three small specimens is five to twenty six (5, 5, 26; mean 12.0); the one individual (juvenile) that was assigned a number of 26 has approximately 20 red "spots" with approximately six additional minute red "flecks" not clearly visible to the unaided eye. Except for this one juvenile, 13 spots is the maximum number for the series, and the mean for the entire series (N = 7) is 11.30. *P. b. belli* usually has a minimum number exceeding 30, including a pair of occipital blotches.

The colors in life were recorded when the body temperatures of the animals were in the range 10-15° C. The ground color of the dorsal surface is black, lightening on the ventro-lateral surfaces, and grading to blackish gray on the ventral surfaces. The dark red spots on the dorsal surface (Fig. 2) vary from bright dark red (Maerz and Paul, 1930, 6-L-1) to deeper dark reds, varying from near Brazil red (4-K-12) and Buccaneer (4-L-12) to Chrysanthemum (5-L-12). With preservation in alcohol, the red color of the spots of *P. belli* fades through pinks to orange-reds and reddish-orange, and finally to orange, yellow, or yellowish. The iris is dark brown in life, striated with black lines radiating more or less from the pupil.

Females may exceed males in body size, as in our sample. The length of the hindleg exceeds the length of the foreleg by a very small amount, on the order of one millimeter or less. The holotype may be representative of the length difference between foreleg and hindleg for males, which appears to be

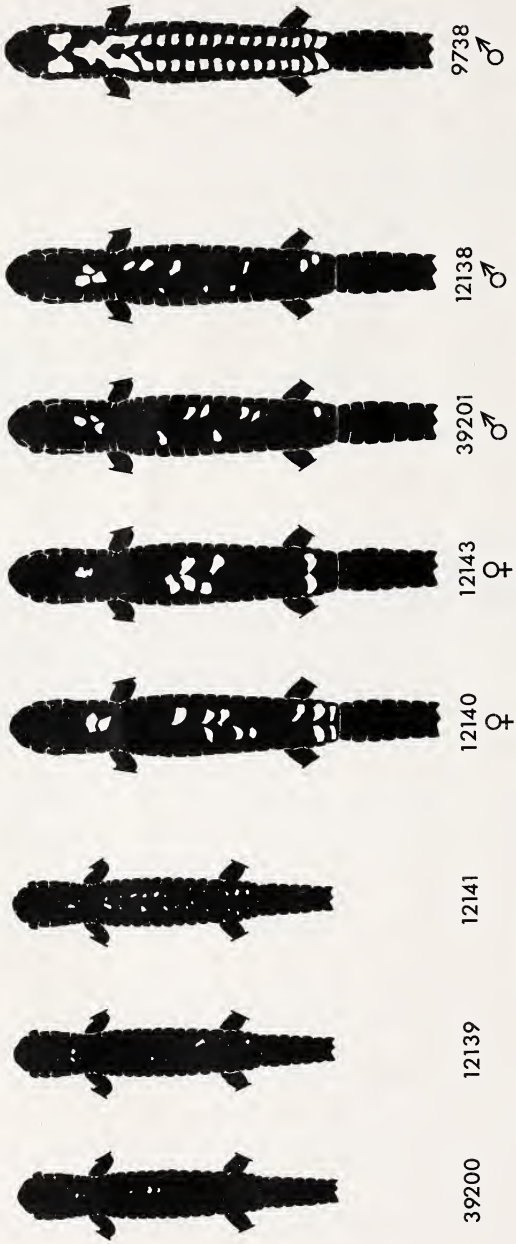


Figure 2. *Pseudoeurycea belli sierraoccidentalis* (type series) from Sonora, and *P. b. belli* (UAZ 9738) from Michoacan. Not drawn to scale.

Figure 3. X-ray (dorsal view) and drawing of right hind foot of *Pseudoeurycea belli sierraoccidentalis* (left) from Sonora, and *P. b. belli* (right) from Jalisco.

negligible when the data are rounded to the nearest mm. The ranges of variation for all seven specimens are 12-20 mm for foreleg and 12-21 mm for hindleg.

There are 12 costal folds and 13 costal grooves, counting one each in axilla and groin. In the three small individuals in the series, the 12th costal groove (counting from front leg toward hind leg) is indistinct.

*Comparisons*: The configuration, juxtaposition and degree of separation of the parasphenoid and vomerine teeth are essentially as in other populations of *P. belli.*

The proportions of some of the body parts of *P. b. sierraoccidentalis* differ from those of comparative material of *P. b. belli* from Jalisco and Michoacan (UAZ 9738, 14805-14811). The toes (web-free toe length) of *b. sierraoccidentalis* are conspicuously short, and their free length is reduced to a half to a third of comparable toes on the same foot of similar size in *b. belli* from Jalisco and Michoacan (Fig. 2). The X-rays of the feet of *b. belli* and *b. sierraoccidentalis* show that the web of *b. sierraoccidentalis* extends anteriad of one additional bone in the digit (Fig. 3).

Overall size of phalanges, legs and feet of *b. sierraoccidentalis* appears to be smaller than in the comparative material of *b. belli* from other regions; because of ontogenetic variation and the small size of our sample, these and some other questions regarding proportional differences between populations can be better answered when larger series of *b. sierraoccidentalis* become available.

We observed the tail to be especially easily dropped on the very slightest pressure against the substratum or other surface, when the animal is excited. These data refer to the type series of *P. belli sierraoccidentalis* (N = 7) in which 57.1 per cent (four out of seven) dropped their tails when they were alive and gently handled—two of four adults (1 ad. ♂, 1 ad. ♀), and two of three immatures. Wake and Dresner (1967), recently reported on tail autotomy in salamanders, and concluded that the degree of tail loss in species with basal tail constriction is more complete but *less frequent* than in their less specialized relatives. *Pseudoeurycea belli sierraoccidentalis*, to the contrary, is a salamander with a pronounced basal constriction, and 57 percent tail loss appears indeed high (see Wake and Dresner, 1967, Table 2) even though the sample available in this case is small (N = 7). The highest tail-break percentage given by Wake and Dresner (1967, Table 2) is 33.4 percent for *Desmognathus fuscus*, a species with a thick-based (non-constricted base) tail; their average for seven non-constricted base species is 23.0%, versus 9.5% for thirteen species with basal constrictions, a difference that is significant at the .001 level. Their sample size varied from N = 46 to N = 757 specimens per species.

Typical of the terrestrial plethodontids with tail base constrictions (the site of tail autotomy), *P. b. sierraoccidentalis* is a "gentle" salamander. It is obvious enough that it exhibits a very definite behavioral control over tail loss,

and that within the family a combination of voluntary and mechanical factors are involved in the breakage of tails at points of constriction, at least in the most highly specialized species (Wake and Dresner, 1967). These authors emphasize in conclusion that the salamander tail is a very important, highly functional organ and suggest that selection has been for behavioral and anatomical adaptations for control of tail loss, rather than for tail loss per se.

*Habitat*: The habitat is in a generally east-west oriented barranca, the upper end of which terminates between the salamander localities and Rancho El Puerto (roughly 5,000 ft). Rancho El Puerto is just to the east of a small divide that parts two drainage systems, and is located at the upper end of another canyon with drainage more to the south and apparently into parts of the state of Chihuahua.

The old road to Yécora is in the bottom of this canyon, which may be as much as 50 but usually is less than 10 yds wide. The canyon floor is loose rock rubble with a stream occasionally flowing over and through it. There is a gradual slope of roughly 30 degrees to either side of the floor, tapering to the 60 degree slope of high canyon walls. The height of the canyon walls varies, but in general they appeared to be approximately 300 ft or more in height at the collection sites.

Numerous short, small side-canyons enter this main canyon from both the north and south-facing slopes, and in three of these (north-facing) the salamanders were located. These side-canyons are quite steep, with many small waterfalls along their courses. It could not be determined if the side-canyons possessed permanent water, but many in the area are in part spring fed. The major stream in the main canyon (barranca) bottom appears to have constant water and is fairly swift, due to a general 20 degree westward downslope.

The substratum on the canyon sides consists of humus-rich soil overlying rather loosely consolidated and often deeply jumbled exfoliated rock (rock rubble) from the canyon walls. In some areas this situation is interrupted by outcroppings of thinly laminated shalelike limestone bluffs. The bedding of the parent material is almost upright and has large vertical fractures. Many large volcanic boulders are scattered along the stream-course, having been carried down from the upper canyon walls.

The present dominant vegetation consists of oaks (*Quercus*, mainly *Q. hypoleucoides*), scattered madrones (*Arbutus mexicana*), and young apache pines (*Pinus englemanni*). It is obvious that the area has been logged at some earlier time, as judged from the number of large old pine stumps. Some of these may have been Chihuahua pines (*Pinus leiophylla*), a prominent species of the Madrean Oak-pine Woodland which was noted nearby on some adjacent higher slopes. Part of the mesic understory and ground cover of forbs was apparently due to the abundance of surface and subsurface water in the area during the summer monsoon. That general conditions are more humid in this particular north-facing habitat than in some others of similar nature nearby, is

further indicated by conspicuously large numbers of the bromeliad *Tillandsia recurvata* on some of the oaks.

The salamanders were collected during a period of several days of torrential summer rains (Sept. 2-7). All of the salamanders found were associated with rather sizable fallen logs, mainly pine, in one instance oak. Some of the logs investigated for the presence of salamanders were as much as four feet in diameter and were for the most part saturated with water and partially buried in the moist humus and soil. The only logs that sheltered salamanders were located in exposures where almost no direct sunlight could strike them at any time of day, and where loose, deep and wet rock rubble also occurred. These areas were located in the southern half of the barranca bottom and within the smaller side canyons of the north-facing slope. Cloacal and substratum temperatures recorded on capture for the four adult salamanders (16.5-17.3°C) varied less than one degree centigrade for all observations. It is unlikely that the diurnal temperature of the underlog salamander microenvironment at the type locality exceeds 20°C during the summer monsoon (June-October).

Although our sample is small, there may be a relationship between the size of the individual and its microhabitat as observed in early September. All of the smaller individuals (three) were found within wet logs, whereas all of the large (adult) individuals (four) were found under large logs in small depressions in the humus and soil.

A small spider was regurgitated by one salamander as it was being preserved on capture.

*Remarks—Itinerary and Logistics*: The salamanders were collected by two field parties in September, 1964. The first party of four—Thomas J. Cox (formerly U.A., Zoology), and John W. Wright, Dr. Kenneth L. Hale (formerly U.A., Anthropology), and Dr. Clyde J. Jones—was trucked by Mr. Cox into the foothills of the Sierra Madre Occidental via Ciudad Obregón and Nuri, with Yécora as destination. The purpose of the trip was to record the Pima language and to collect vertebrates encountered enroute. Dr. Jones collected a small black salamander in a wet log streamside and roadside to the old road to Yécora, above Nuri (the type locality). The specimen was collected during the evening, on a long return hike from Yécora to the vicinity of Santa Ana (below the type locality), where the truck had stopped the day before. As the party was pressed for time, it returned directly to the University of Arizona on September 5.

On the following morning, September 6, the second field party (authors) left Tucson for Yécora with bush-pilot Mr. David Vactor of Tucson, in Mr. Vactor's Cessna 180, and landed on the air strip at Yécora at 11:00 a.m. Pack animals were obtained from Mr. Gordon MacMurray of Yécora and the salamander locality was reached that night during a lengthy rainstorm. On the morning of September 7, a series of six additional individuals of *Pseudoeurycea belli* (four adults, two young) were collected in the area, all in or under wet (soaked) logs of pine and oak. We returned to Yécora before dark and headed

immediately for Tucson by air via Hermosillo, with four of the six salamanders alive in wet cloth sacks on ice in a small styrofoam bucket; the other two salamanders were preserved on capture.

*Remarks—Species versus Subspecies*: The Sonoran population described here is allopatric with *Pseudoeurycea belli* to the south, and the geographic gap is a respectable distance (see *Biogeography*, below). We note that Taylor's (1938) *P. gigantea* from Veracruz is less distinct from *P. belli* than is the Sonoran population described here as a subspecies. If Taylor's allocation to species (*P. gigantea*) is correct for the Veracruz population, it would appear that the Sonoran population could be expected to be specifically distinct from *P. belli,* the relationship which we regard at this time as least likely.

Taylor's (1938) opinion on *P. gigantea* was contrary to Dunn's (1926). Dunn originally considered the material of Taylor's *P. gigantea* (including live animals Dunn collected in Veracruz) to be within the range of variation of *P. belli. Pseudoeurycea gigantea* Taylor is distinctive and allopatric. The question is whether it should be regarded as a species or subspecies.

*Remarks—Southwestern Mountains*: With the discovery of *Pseudoeurycea* in Sonora, the old record of *Oedipus bellii* from Arizona obviously deserves reconsideration. Dunn (1926:360) listed the species for Arizona in his monograph on the Plethodontidae, but gave the matter no further consideration than the following line in his listing of localities: "United States: Arizona: Ft. Whipple 3 (U.S.N.M., uncatalogued, now lost)." Taylor (1938:266) stated that the record of this species from Arizona should be questioned, and that, although listed by Dunn, it was "apparently doubted by him." Later Taylor (1941) reiterated his conclusion, and subsequently (Lowe, 1955) there seemed no point in attempting to revive the old question, since field work during 1950-1955 in the Bradshaw Mountains and others had been unsuccessful.

Since 1950 one or more of us have made periodic and unsuccessful trips into the Bradshaw Mountain area of Arizona and into other Arizona, New Mexico, Sonora, and Sinaloa ranges during the summer monsoon, in an effort to locate plethodontid salamanders at or near the provenance of the lost USNM *Oedipus bellii* from Fort Whipple (vicinity Prescott), *fide* Dunn (1926). A still further concentrated effort is now indicated for Arizona-New Mexico-Sonora, in ranges such as the Bradshaws, Chiricahuas, Pinaleños, and Mogollons, which are Cordillieran outliers positioned between the Sierra Madre and the Rockies. Some of the attendant seasonal field problems encountered in such work in the Southwest and in Mexico are indicated by Taylor (1944: 216), Lowe (1950:96, 1955:250), and Stebbins (1951:79).

*Biogeography*: The discovery of *Pseudoeurycea belli* in the Sierra Madre Occidental near its northern end in Sonora, is of biogeographic interest and importance. Plethodontid salamanders have not been reported previously from the west coast of Mexico north of Sierra de Nayarit (*Oedipus bellii*, Gadow 1905, unconfirmed). The locality in Sonora, near the confluence of the state lines of Sonora-Chihuahua-Sinaloa, extends the known range of the species

roughly 550 miles[4] northward from the previously recorded locality (Sierra de Nayarit), and across nearly the entirety of the south-north oriented Sierra Madre Occidental.

While Taylor (1944:212) considered such an eventuality as somewhat dubious, Dunn (1926, and elsewhere) either did not consider the situation possible or, less likely, he did not consider it at all. Dunn's (1926) apparent dismissal of the old "Arizona" specimens of *Oedipus bellii* (USNM, lost) as of any biogeographic importance is understandable. In addition to representing an unlikely provenance for what was then thought to be a species occurring only in "South Central Mexico," such a unique Arizona occurrence of *Oedipus bellii* (= *Pseudoeurycea belli*) might have been considered contrary to parts of his thesis on the origin and evolution of the family Plethodontidae.

According to Wake's (1966) recent reclassification of the family Plethodontidae, *Pseudoeurycea* is one of the genera in the supergenus *Bolitoglossa*, in the tribe Bolitoglossini in the subfamily Plethodontinae. Wake considers bolitoglossine salamanders (supergenera *Batrachoseps*, *Hydromantes*, and *Bolitoglossa*, including *Pseudoeurycea*) to have been established early as a group, possibly in early Tertiary or even late Cretaceous. He places that event, and other major evolutionary events in the Plethodontidae, in Appalachia in eastern North America, as did Wilder and Dunn (1920) and Dunn (1926). According to Wake (1966), the plethodonine salamanders (genera *Aneides, Ensatina, Plethodon*)—the second terrestrial group—diverged in Appalachia later than the bolitoglossine divergence. While plethodonines occur today in both western and eastern North America, the bolitoglossines occur only in western North America.

The present discovery of *Pseudoeurycea* near the juncture of the 30th parallel and 110th meridian in Sonora, Mexico, while surprising as a sizable as well as an unexpected northwestward extension of a supposed southern genus virtually into the United States, is consistent with major outlines of bolitoglossine salamander evolution as described by Wake (1966). It is also consistent with hypotheses in the recent report by Regal (1966), published simultaneously with that of Wake, in which Regal places the geography of the major evolutionary events in the family Plethodontidae in western rather than in eastern North America. While Wake (1963, 1966) agrees that the indirect evidence available warrants a hypothesis that western North America has been an important center of plethodontid radiation, he argues in support of Dunn's (1926) thesis that the basic radiation was centered in eastern North America (Wake, 1966).

## ACKNOWLEDGMENTS

Mr. Alfred P. Gardner (Louisiana State University, Zoology) kindly collected for us during the summer of 1965 a large series of *Pseudoeurycea*

[4]Map distance between Yécora and Tepic varies with the cartographer and publisher; it is on the order of 550 ± 25 airline miles.

*belli* in the Nevado de Colima, Jalisco, Mexico. Figures 2 and 3 were drawn by Mr. James L. Patton, Department of Zoology, The University of Arizona.

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# A NEW SUBFAMILY OF BLIND BEETLE FROM IDAHO ICE CAVES WITH NOTES ON ITS BIONOMICS AND EVOLUTION (COLEOPTERA: LEIODIDAE)

*By* RICHARD L. WESTCOTT

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# A NEW SUBFAMILY OF BLIND BEETLE FROM IDAHO ICE CAVES WITH NOTES ON ITS BIONOMICS AND EVOLUTION (COLEOPTERA: LEIODIDAE)

*By* Richard L. Westcott[1]

Abstract: A new genus and species, *Glacicavicola bathyscioides*, is described and a new subfamily, Glacicavicolinae, is erected. Based upon structure of the front coxal cavities, placement of the hind coxae and structure of the male genitalia, this subfamily appears most closely related to Catopocerinae. Specimens were collected in southern Idaho from three widely separated lava tube ice caves, and were found in direct contact with the ice. The caves are briefly described. Considerations are given as to the evolution and means of dispersal of this new beetle. It appears to be an extremely specialized glacial relict which has extended its range through the porous lavas in which the caves occur.

During the summer of 1965 I discovered a remarkable anophthalmic beetle while exploring a lava tube ice cave in the eastern Snake River Plain of southern Idaho. This cave beetle, which represents a new genus and species, creates, in my opinion, a need for erecting a new subfamily.

I am grateful to W. F. Barr, University of Idaho, for his many helpful suggestions in the preparation of this paper and to Jim Papadakis, Crystal Ice Caves, for allowing access to and providing information about the caves. Thanks are given to T. C. Barr, Jr., University of Kentucky, M. H. Hatch, University of Washington, Martin Prinz, Tufts University, and R. E. Williams, University of Idaho, for information pertaining to this study. I would like also to acknowledge the assistance of my colleague, L. S. Hawkins, Jr., who accompanied me in the exciting discovery of this beetle. Figure one was drawn by Nellie Lambley, University of Idaho.

## GLACICAVICOLINAE, New Subfamily

A subfamily of Leiodidae characterized by the following characters: dorsal surface virtually glabrous; antennae subclavate, eleven-segmented, scape much longer than any other segment, eighth segment not distinctly narrower or shorter than seventh or ninth; terminal segment of maxillary palpi large, longer than any other segment, somewhat fusiform; front coxae elongate, cylindric-conic, contiguous, inserted near hind margin of prothorax, cavities widely open behind; mesocoxae globose, contiguous; metacoxae oval, transverse, widely separated; tarsal formula 5-5-5; abdomen with all but last two visible tergites membranous, with five (♀) or six (♂) visible sternites.

This beetle belongs in the superfamily Staphylinoidea, according to the

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characters given to that group by Crowson (1955), but its assignment to family presents some difficulty, primarily because considerable disagreement exists in defining the families of Staphylinoidea. The staphylinid-silphid-leptodirid-leiodid complex, to which this beetle certainly belongs, is particularly difficult to define, and to do so is beyond the scope of this paper. It seems best to place this beetle in the family Leiodidae, as delimited by Hatch (1957), although one of the main characteristics of this family, namely that the eighth antennal segment is conspicuously shorter and narrower than the seventh and ninth, does not apply. The structure of the male genitalia agrees closely with that found among many of the Leiodidae, particularly those of the subfamilies Catopocerinae, Bathysciinae, and Catopinae.

The subfamily Glacicavicolinae bears a striking resemblance to many of the elongate cavernicolous species of the almost exclusively European subfamily Bathysciinae. However, the two can readily be separated by the structure of the front coxal cavities, which are closed behind in the Bathysciinae and widely open behind in the Glacicavicolinae. Furthermore the bathysciines have the terminal segment of the maxillary palpi awl-shaped or conical, short, and much smaller than segments two or three. The Leiodidae have the front coxal cavities closed behind except in the Catopocerinae and some species of *Hydnobius* (Leiodinae). The Catopocerinae appear almost unique in having the hind coxae separated, and based upon this premise Glacicavicolinae might well be placed near them. However, members of the Catopocerinae always have the eighth antennal segment distinctly smaller than the seventh or ninth. Both the Catopocerinae and Glacicavicolinae lack antennal vesicles (see Crowson, 1955) and possess widely open procoxal cavities. On this basis they might be placed in the Silphidae. Crowson (1955) has referred Catopocerinae to this family. However, the structure of the male genitalia of both subfamilies strongly suggests a leiodid affinity.

Hatch (1933) and Arnett (1960) recognize the family Leptodiridae, though there is some difference of opinion on placement of certain subfamilies. Hatch (1933) describes the Leptodiridae to include generally fragile species with long appendages and thin integuments, while the Leiodidae include stocky species with shorter appendages and heavier integuments. Using this as a criterion, the Glacicavicolinae would fall into the leptodirid section. Hatch (1957) subsequently places the leptodirids under Leiodidae. For further discussion of the staphylinid-silphid-leiodid complex, the reader is referred to Brown (1933), Hatch (1927), and Horn (1880).

The Glacicavicolinae also bear superficial resemblance to the Brathinidae. Both groups have the procoxal cavities open behind and the structure of the maxillary palpi is very similar. However, the male genitalia of Brathinidae are of the staphylinid type, lacking a *pars basalis*, and of the visible abdominal tergites, all but the basal are sclerotized, while in the Glacicavicolinae the genitalia possess a *pars basalis* and all of the visible abdominal tergites are membranous except for the ultimate and a portion of the penultimate. Further-

more, in the Brathinidae the hind coxae are contiguous, conical, and prominent internally, while the Glacicavicolinae have the hind coxae widely separated, oval, and not prominent. The antennal scape in the Brathinidae does not exhibit the proportionately great length evident in the Glacicavicolinae.

The placement herein of Glacicavicolinae is, admittedly, an arbitrary one and I would not argue with those who might wish to define it differently. However, it is firmly believed that its affinities lie with the Silphidae or Leiodidae, as delimited by Hatch (1957), rather than the Brathinidae or Staphylinidae, as defined by Arnett (1960). Perhaps this strange beetle may represent an entirely new family, but to classify it as such at this time would, I believe, obscure its relationships.

## **Glacicavicola** new genus

Type species: *Glacicavicola bathyscioides* new species.

Head oval, elongate, sharply constricted posteriorly into a well-defined neck; gula roughly triangular, sutures meeting near middle of head, then extending to submentum; eyes absent; labial palpi small, terminal segment cylindrical; antennae extremely long and with very long hairs, inserted dorsolaterally just in front of middle of head under a slightly raised portion of frons which extends forward as a slight ridge; apical swelling of segments nine and ten together with fusiform terminal segment forming a slight club.

Thorax with pronotum longer than wide, sides smoothly rounded; scutellum large, triangular; mesosternum keeled, sharply constricted anteriorly where it is much narrower than the pronotum and bears a depression which is almost divided medially by the pronounced apical portion of the keel and a marginal, backward-projecting triangular piece, so that in lateral view it usually appears notched.

Elytra much longer than wide, much wider than pronotum, inflated, very convex, fused; epipleural fold apparent only on apical half, ending a short distance before apex; hindwings absent.

Legs extremely long, hind legs longer than body, femora clavate, all tibiae with two moderately-developed spurs of equal size; male with patches of tenet hairs beneath pro- and mesotarsi; tarsal claws long, sickle-shaped.

Abdomen with first two visible sternites immovably fused, the suture between them distinct.

## **Glacicavicola bathyscioides** new species

Figs. 1-5

*Male*: Elongate, length almost twice width, antlike, very fragile, exhibiting false physogastry; color shining brownish-red, elytra translucent, with very faint lateral spots which are particularly noticeable on apical half; setae scarce on dorsum.

Head almost twice as long as wide, widest in front of middle, convex;

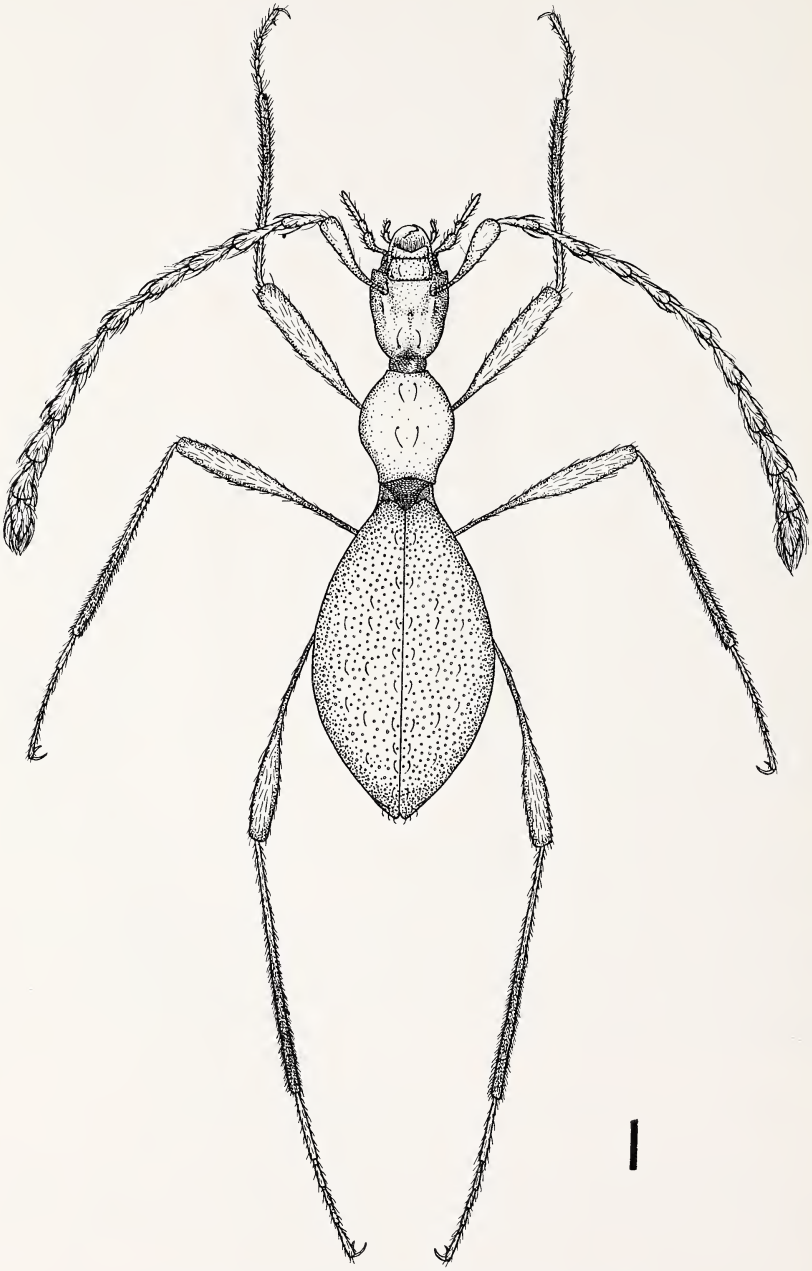


Figure 1. *Glacicavicola bathyscioides*, new species.

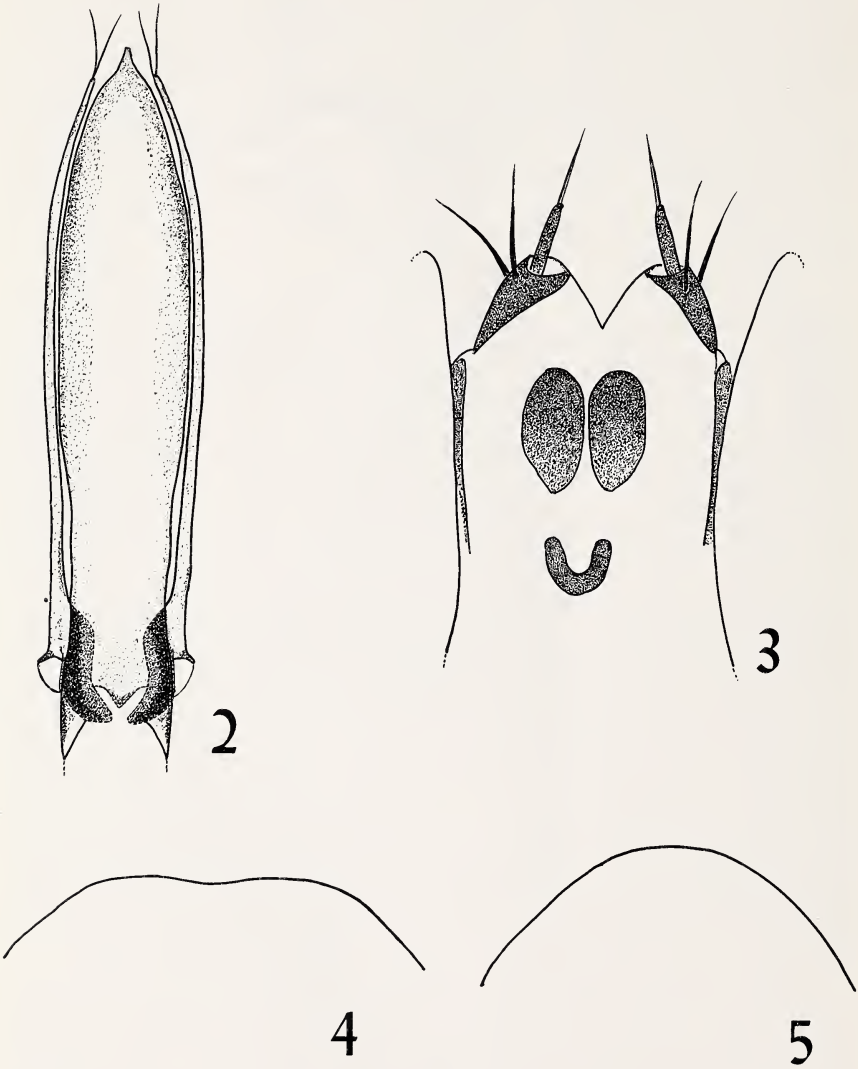
surface unevenly microreticulate, becoming rugose on neck, dorsal surface of epicranium with a faint median longitudinal depression, with setigerous punctures as follows: a widely-spaced pair immediately behind frontoclypeal suture, one just mesad of ridge in front of each antennal insertion, one just caudomesad of each antennal insertion, all bearing a short, recurved seta; and a widely spaced pair between caudal end of median depression and neck, each bearing a conspicuous, long, recurved seta; a few, mostly long, setae present on clypeus, labrum, mentum, submentum, and anterior ventrolateral portion of epicranium; maxillary palpi moderately setose from apex of antepenultimate segment to apical portion of ultimate which is glabrous; ratio of lengths of last three segments 0.8:0.5:1; antennae almost as long as body, approximate ratio of lengths of segments 2.2:1.1:1.3:1.3:1.4:1.5:1.5:1.6:1.4:1:1, scape and pedicel with few hairs, segments 3-6 moderately hairy, remaining segments more densely pubescent.

Thorax with pronotum one and one-fifth times as long as wide, widest at middle, wider at base than apex; surface slightly convex, evenly microreticulate, becoming smooth at sides, with a pair of setigerous punctures close behind anterior margin; sides broadly rounded for apical three-fourths, then converging toward base; anterior margin evenly curved, fitting contour of neck; posterior margin slightly emarginate. Scutellum large, triangular; surface rugose. Propleura smooth. Prosternum faintly alutaceous, with two long and several shorter setae near front margin, which bears a series of minute, forward-projecting setae. Mesosternal depression bearing dense, long, golden pile.

Legs long and slender except for femoral clubs, which make up seven-tenths of the profemora, one-half the mesofemora, and slightly over two-fifths of the metafemora; ratio of leg lengths (excluding coxa and trochanter) approximately 6:7:9; pro- and mesofemora with ventral row of long hairs which increase in length for about basal three-fourths, hairs of apical fourth shorter and equal to those covering other surfaces of club, posterior surfaces with fewer, shorter hairs; tibiae about equal in length to femora, pro- and mesotibiae bearing a preapical comb of stout setae on anterior and posterior faces; protarsi with apical segment longest, twice as long as basal segment, basal three segments slightly dilated and bearing patches of trumpet-shaped tenet hairs; mesotarsi with basal segment subequal in length to apical segment, basal two segments bearing trumpet-shaped tenet hairs in sparser patches than on protarsi; basal segment of metatarsi noticeably longer than apical segment.

Elytra swollen, elongate, one and three-fourths times as long as wide, twice as wide as pronotum; surface covered with fine, irregularly, widely spaced punctures except at sides; apical fourth, sides, and a narrow strip on either side of suture exhibiting an extremely fine granular appearance; disc with a few, fine, recurved hairs which appear to be arranged in three longitudinal rows beginning near suture, a few small, fine submarginal hairs on apical fifth, mostly in immediate vicinity of apex; sides broadly overlapping

abdomen; lateral margins sinuate near middle then gradually, arcuately converging to separately, narrowly rounded apices.




Figures 2-5: *Glacicavicola bathyscioides.* 2: male genitalia. 3: median portion of female genitalia. 4: posterior margin of fifth visible (penultimate) abdominal sternite of male. 5: posterior margin of fifth visible (ultimate) abdominal sternite of female.

Abdomen with sternum finely alutaceous, sparsely clothed with long, suberect hairs; fifth visible sternite with apex broadly, shallowly emarginate, almost subtruncate. Genitalia as in Fig. 2.

Length: 5.9 mm. Width: 1.9 mm.

*Female*: Agrees with description of male except for the following: pronotum with additional pair of setigerous punctures at middle. Protarsi not dilated, pro- and mesotarsi without tenet hairs. Abdomen with apical margin of fifth (last) visible sternite broadly rounded. Genitalia as in Fig. 3.

Length: 5.9 mm. Width: 1.9 mm.

*Type Material and Localities*: HOLOTYPE male, Crystal Falls Cave, Clark County, Idaho, June 11, 1965 (R. L. Westcott & L. S. Hawkins, Jr.); ALLOTYPE female, same locality, June 12, 1965 (R. L. Westcott); both deposited in the California Academy of Sciences on indefinite loan from the University of Idaho. PARATYPES: Same locality as holotype and allotype: 1 ♂, 3 ♀♀, same data as holotype; 6 ♂♂, 4 ♀♀, same data as allotype; 16 ♂♂, 14 ♀♀, VII-16-1965 (R. L. Westcott); 1 ♂, 2 ♀♀, VIII-7-1965 (R. L. Westcott); 1 ♂, VII-5-1966 (W. F. Barr); 2 ♀♀, VI-8-1967 (R. L. & J. A. Westcott).

The following specimens were not designated as paratypes: IDAHO: Butte County: Boy Scout Cave, Craters of the Moon National Monument: 1 ♂, 2 ♀♀, VII-18-1965 (R. L. Westcott); 6 ♂♂, 6 ♀♀, VII-17-1967 (D. S. Horning, Jr.). Power County: Crystal Ice Caves: 3 ♂♂, 2 ♀♀, VI-17-1965 (R. L. Westcott & L. S. Hawkins, Jr.); 6 ♂♂, 4 ♀♀, IX-1-1965 (R. L. Westcott).

Paratypes are deposited in the collections of the American Museum of Natural History; British Museum (Natural History); California Academy of Sciences; Chicago Natural History Museum; Entomology Research Institute, Canada Department of Agriculture, Ottawa; Los Angeles County Museum of Natural History; Museum of Comparative Zoology, Harvard University; Purdue University; United States National Museum; University of California, Davis; University of Idaho; University of Washington; T. C. Barr, Jr. (University of Kentucky); G. H. Nelson (Kansas City); and the writer.

*Variability*: Relatively little variation in size, form, or color can be detected. Perhaps most obvious is a variability in the size of the notch formed between the independently rounded elytral apices. Females from Crystal Ice Caves and Boy Scout Cave usually have the last visible abdominal sternite more broadly rounded or even truncate. Some specimens have been taken which are testaceous in color, but these undoubtedly are teneral adults.

Variation in sculpture and setal arrangement is evident. There are differences in the degree of fine granulation present on certain portions of the elytra. This character appears to be almost lacking in some specimens from Crystal Falls Cave, but it is readily observable in specimens from Crystal Ice Caves. However, the two populations do not diverge significantly enough to warrant subspecific differentiation.

An interesting variation in setal pattern is exhibited by the setigerous punctures of the head and pronotum, particularly the latter. The setigerous punctures of the dorsal surface of the epicranium almost always conform to the pattern exhibited by the holotype. In referring to these structures, the anterior and posterior locations are not morphological but positional, owing to the prognathous condition of the head. The setae born by these punctures are not of uniform size. Those immediately behind the frontoclypeal suture and those caudomesad of the antennal insertions are recurved, of about the same size, and usually quite evident when viewed at the correct angle with proper lighting. Those in front of the antennal insertions are not always recurved, usually much smaller and difficult to see, while the posterior pair are almost always much larger than any of the other setae, strongly recurved forward, and with the anterior portion in contact with the surface of the head. In addition, there may be present a few minute setae, especially on the median discal area of the epicranium. Quite often there is a pair located not far in front of the large posterior setae. A few specimens possess extremely reduced posterior setae and some appear to have the setigerous puncture lacking on one side.

A much greater degree of variation is evident in the setal pattern of the pronotum. Over half of the specimens examined exhibit the same pattern as the allotype, possessing an anterior and median pair of setigerous punctures, each of which bears a moderately long, backward-recurving seta. Other specimens exhibit wide variation, as shown in Table 1. Each setigerous puncture of a pair is not always evenly placed with respect to its counterpart. The anterior pair are almost always evenly placed, but a considerable number of specimens show anterior or posterior displacement of one of the median punctures, and one

TABLE I

| PATTERN OF SETIGEROUS PUNCTURES | SPECIMENS EXAMINED | |
|---|---|---|
| | MALES | FEMALES |
| All present | 16 | 25 |
| A | 6 | 2 |
| P | 0 | 1 |
| RA | 1 | 2 |
| LA | 1 | 0 |
| RA, P | 1 | 2 |
| LA, P | 6 | 0 |
| A, RP | 2 | 2 |
| A, LP | 2 | 2 |
| RA, LP | 1 | 0 |
| LA, LP | 0 | 1 |
| LA, RP | 2 | 0 |
| None present | 1 | 1 |
| TOTAL | 38 | 38 |

Variation in setal pattern of pronotum (cf. Fig. 1). R = right, L = left, A = anterior, P = posterior. A lone "A" or "R" indicates the presence of both members of the pair.

specimen exhibits a lateral displacement. Two of the specimens examined have an extra anterior setigerous puncture on one side. Care must be taken to look for the punctures themselves, as the setae often break off.

A paramere of the male genitalia may possess an additional seta located a short distance below the apical pair of setae.

## BIONOMICS

*Glacicavicola bathyscioides* has been taken from three widely separated lava tube ice caves on the eastern Snake River Plain of Idaho. The primary collecting site was Crystal Falls Cave, but specimens were taken also from Boy Scout Cave and Crystal Ice Caves, which are approximately 160 km and 184 km respectively from Crystal Falls Cave.

Crystal Falls Cave, about 30 km northeast of Dubois, is a lava tube cave located at an elevation of approximately 1891 m (6200 ft) in an area of numerous craters and lava outcroppings. The surrounding area exhibits a more extensive vegetation than that found at the other caves mentioned, which may indicate an older age for this cave. It consists of at least three levels, only one of which was readily accessible. This section was estimated to be 305 m in length, including the spacious chamber into which the large entrance opens. At the far end of this chamber, a much smaller opening leads downward into the portion of the lava tube in which permanent ice is found. Here there is an extensive ice floor and several ice mounds and stalagmites. During the summer and early fall, considerable melting takes place except in the terminal portion of the cave. Maximum-minimum thermometer readings taken where melting occurs showed the temperature to fluctuate by no more than a degree from freezing during a period from July to mid-September, but the winter low during the 1966-67 season was −5.5°C.

Approximately 160 km southwest, at an elevation of about 1769 m (5800 ft) in Craters of the Moon National Monument, is Boy Scout Cave. It lies in an area of numerous lava flows and sparse vegetation (cf. Stearns, 1947). This lava tube cave occurs in pahoehoe lava, is small, and has permanent ice only in limited areas.

Crystal Ice Caves are located approximately 64 km to the south of Boy Scout Cave in a small lava field west of Aberdeen at an elevation of approximately 1525 m (5000 ft). They occur in the southern portion of a volcanic rift known as the Great Rift. The lavas of Craters of the Moon also flowed from this rift. Unlike the other caves, Crystal Ice Caves were formed by great explosions which took place along the Great Rift. The ice in these caves presents a fantastic display, occurring in such forms as stalactites and stalagmites of all shapes and sizes, delicate crystals, ice falls, and a solid floor (Fig. 6). The most interesting caves were virtually inaccessible without special equipment, but through the efforts of Jim Papadakis they are now open to the public.

Other lava tube caves were examined, but none of them appeared to

contain appreciable amounts of permanent ice, if any, and no beetles were found. Shoshone Ice Cave, north of Twin Falls, has extensive permanent ice, but due to interference by man there was a long period when this ice was absent. No evidence of *G. bathyscioides* was found there.

Figure 6. Ice formations at Crystal Ice Caves. Photo courtesy of Jim Papadakis.

All of the beetles have been found either on the ice, where they crawl slowly, or floating in meltwater above the ice floor, where many drown. Perhaps the beetles occur on the walls and ceilings of the caves and fall onto the ice, where they are readily visible. They would be extremely difficult to see on the lava rock. They appear to be particularly partial to ice mounds or large ice stalagmites, the former frequently harboring a variety of arthropods, dead as well as alive. Those arthropods which likely are regular inhabitants of the ice caves include staphylinid beetles, collembolans of the family Entomobryidae, a dipluran of the family Japygidae, several small flies of uncertain affinity, a phalangid, and a recently described millipede, *Idagona westcotti* Buckett & Gardner (1967). One staphylinid, *Quedius spelaeus* Horn, has also been reported from lava tube caves in western Washington (Halliday, 1963). Anthomyiid flies, ichneumonid wasps, and coleopterous larvae of the family Cantharidae have been found, and these represent epigean insects which are classified as cave accidentals. These forms cannot live long in the caves, but doubtless serve as an important source of food for some cavernicoles. Small staphylinids of the subfamily Aleocharinae were observed feeding on dead cave accidentals as well as on a white fungus that grows abundantly on organic matter in the caves.

Very little of the biology of *Glacicavicola bathyscioides* has been ascertained. Only a single mating has been observed and this took place in the presence of an additional "audience" of half a dozen beetles about seven feet up a stalagmite. This may suggest that a sex-attractant is involved, which would certainly not be surprising considering these beetles are blind. During the summer of 1967, Don Horning, University of California at Davis, discovered several *G. bathyscioides* in Boy Scout Cave and was fortunate enough to observe a single beetle chewing on sclerotized portions of a dead individual of the same species. Fungus was observed growing on the dead beetle. Further observations are necessary before elaboration can be made upon feeding habits as well as other aspects of the biology of this unique cavernicole.

## EVOLUTION

Terrestrial cavernicoles are considered to have evolved from forms which lived in such media as the soil (endogeans), snow-pockets (nivicoles), mosses (muscicoles), and humus or duff (humicoles). These media approximate the uniform, stable environment found in most caves. For a classification of cave-dwellers, the reader is referred to Barr (1964) and Vandel (1965).

*Glacicavicola bathyscioides* is an obligate cavernicole (troglobite) with specialized features which make hypothesizing its phylogeny and evolution difficult. However, its lack of known close epigean relatives may imply a great antiquity, and the fact that it has been found associated with ice strongly suggests that it represents a glacial relict.

Following the terminology of Vandel (1965), it is postulated that the phyletic line of *Glacicavicola* underwent a long period of "preparation" for a

cavernicolous existence, possibly beginning sometime during the first half of the Tertiary when the climate was more tropical in northern latitudes. The onslaught of cooler weather, which forecast the beginning of the Ice Ages, invoked the southward migration of many animals, while others gradually adjusted to the changing climate. Probably as a result of physiological regression, some terrestrial forms, such as any of those mentioned previously, became dependent upon a more humid environment. As the climate remained cold, glaciers came into being, and many of these animals could not survive. However, some were able to exist as nivicoles in the cool, moist, periglacial environment. Some, such as the ancestral glacicavicolines, may have even inhabited the glaciers themselves. Many nivicoles exist today, and several cavernicolous bathysciines are known to inhabit ice caves in the mountains of Europe (Vandel, 1965).

The eastern Snake River Plain, where *G. bathyscioides* lives, is largely underlain with basalt of different ages (Stearns *et al.*, 1939; Mundorff *et al.*, 1964). Much of this is exposed, particularly in areas of the more recent lava flows. Many caves exist throughout the area, the majority of them being lava tubes. Some of them contain ice the year around. The Snake River basalt is believed to range in age from Pliocene to Recent, and considering the plain as a whole, eruptions have continued from earliest Pleistocene to comparatively recent times (Hamilton, 1965). At least twice during the Pleistocene, glaciers have occupied areas not far from Crystal Falls Cave. Extensive glaciation was located in the Yellowstone area to the east and, to a lesser degree, north in the region of the Continental Divide (Stearns *et al.*, 1939).

It is not difficult to imagine the ancestral glacicavicolines taking refuge in the lava tube ice caves from the warmer, more arid climate which brought about a rather rapid recession of the glaciers. Conditions were no doubt favorable for this more than once during the Pleistocene, and it seems likely that this refuge began during one of the earlier interglacial periods. Had it occurred after the last and most extensive glacial period, it seems doubtful if *G. bathyscioides* would yet have attained such a high degree of specialization.

From this discussion it can be hyposthesized that *G. bathyscioides* had its origin somewhere in the vicinity of Crystal Falls Cave, possibly in the once glaciated region just to the north or east, and from there it spread westward and southward to caves at lower elevations.

## DISPERSAL

*Glacicavicola bathyscioides* occurs in caves which are separated by distances of over 160 km, thus creating a problem in explaining its means of extending its range. Since its extreme specialization must involve a physiology which renders it fit to live only in an underground environment, it is highly improbable that any extension of its range has been made above ground, either by accident or otherwise. However, this possibility must be explored. An unsuccessful attempt to bring these beetles out of the caves and keep them

alive without some form of protection from the epigean environment leads me to believe that even a brief exposure to warm temperatures and/or sunlight is fatal. Thus it must be assumed that *G. bathyscioides* has extended its range by underground dispersal.

One of the most extensive groundwater systems known lies beneath the Snake River Plain (Mundorff *et al.,* 1964). Water flow beneath the plain is generally in a southwesterly direction and according to R. E. Williams (pers. comm.), an average movement of about 11 feet per day is not unreasonable. Under isolated conditions the rate of flow may be much higher. Groundwater in the lava beneath the plain occupies pores between unconsolidated materials such as cinders and blocks, joints and fractures, and irregular openings in and between lava flows (Mundorff *et al.,* 1964; Olmsted, 1963). Such irregularities occur above the water table as well and numerous cracks and crevices are apparent on the surface of the lava flows and in the lava tube caves. It is easy to imagine a small beetle, such as *G. bathyscioides,* being able to move or be carried considerable distances through this system of subterranean channels in a relatively short period of time.

Another means of dispersal can be explored. It was mentioned previously that the ancestral glacicavicolines probably took refuge in the ice caves after one of the earlier glacial periods. There they may have remained until, during some subsequent glacial advance, the climate became cold and wet enough for them to move about at or near ground level. However, for reasons already mentioned, this explanation appears less likely.

Either explanation (particularly the former) poses the question of how food is obtained under such extreme conditions. However, it would seem that the food problem is not a limiting factor, since Vandel (1965) has reported that some bathysciines have been kept alive for eight months without food and certain troglobites are known to derive nourishment from organic or mineral deposits in silt or clay.

The foregoing discussions concerning the evolution and dispersal of *G. bathyscioides* are by no means complete, but I hope they may serve as a stimulus for further investigation into this most interesting subject.

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# TERTIARY BIRDS FROM LAGUNA HILLS, ORANGE COUNTY, CALIFORNIA

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DOROTHY M. HALMOS
*Editor*

# TERTIARY BIRDS FROM LAGUNA HILLS, ORANGE COUNTY, CALIFORNIA

*By* HILDEGARDE HOWARD[1]

ABSTRACT: Approximately 120 of more than 200 avian bone fragments collected from one locality in Leisure World, Laguna Hills, California, can be given family assignment. At least 19 species are represented, but only nine are specifically assigned, even on a tentative basis. One genus and four species are newly described. The avifauna does not relate to that of any one of the other Tertiary localities in southern California, but individual species show greater resemblance to those of Middle and Late Miocene than to those of the Pliocene.

## INTRODUCTION

Marine deposits in the Laguna Hills area of Orange County, California, have yielded fish, bird and mammal fossils of possibly two epochs of the Tertiary. As previously noted (Howard, 1966a), remains of the Pliocene flightless auk, *Mancalla*, occur at two sites, whereas a distinctly less specialized, possibly ancestral mancallid, genus *Praemancalla*, is found in association with Miocene desmostylian remains at a third locality, Los Angeles County Museum of Natural History (LACM) Vertebrate Paleontology locality no. 1945. The sites lie within the senior citizens' community of Leisure World, about a mile and a quarter southwest of the town of El Toro. LACM locality 1945 is approximately one-quarter mile north of Aliso Creek, which, in this area, runs in a southwest direction; the other localities (now listed as LACM 65120 and 65121) are at a somewhat higher elevation south of the creek and slightly east of LACM 1945. The three localities were uncovered for a short time only, as hillsides were cut away and excavations made for the development of new units of the community. Since one site was closed to view before another was revealed, stratigraphic studies have been incomplete.

Most of the bones from LACM locality 1945 are highly mineralized, smooth-textured, and of dark brown or brownish gray color. A few bones are markedly water-worn and have adhering to them a hard matrix, different from the surrounding sediments. Three or four bones of lighter color and rougher texture are seemingly less mineralized than the others. At localities LACM 65120 and 65121, most of the bones are light in color, often mottled, and of rough, uneven surface.

*Locality LACM 1945*: The present study is confined to the specimens recovered from LACM locality 1945. The main collections were made by the museum in August and December, 1964, with some additions up to the time the site became unavailable, during January, 1965. As listed in the LACM records, field data for this locality read as follows: "1¼ miles SW of the town of El Toro; ¼ mile N of Aliso Creek, on the property of Leisure World Co.,

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Figure 1. Excavations at LACM locality 1945, Leisure World, December, 1964.

SW/4 of NE/4 of SW/4, Sec. 34, T 6 S, R 8 W, Orange County, Calif., San Juan Capistrano quadrangle." The field notes of Mr. W. Earl Calhoun, whose watchfulness during building operations made possible much of the fossil collecting, supply the following information regarding the location of the site with respect to the present street and building pattern at Leisure World: "Strata run in a line between Bldg. 221 on one side and Bldgs. 211 to 216 on the other side in a north-south direction, dropping approx. 15° to east." The best locality for bird bones was at the northwest side of building 215 Avenida Majorca. (See Fig. 1.)

*Acknowledgments*: The Museum is grateful to Mr. Ross W. Cortese and Rossmoor Leisure World, Laguna Hills, for the opportunity to collect while work was under way for new units. We are particularly appreciative of the efforts of Mr. W. Earl Calhoun in our behalf; and our thanks go, also, to the several unknown residents who turned over specimens for the benefit of the Museum.

The type of *Eremochen russelli* was available on loan through the courtesy of the University of Oregon. Recent skeletons of *Aethia, Cyclorrhynchus* and *Plautus* were kindly loaned by the California Museum of Vertebrate Zoology, Berkeley, Calif., and the United States National Museum.

Photographs were made by Mr. Mike Hatchimonji, Senior Photographer, Los Angeles County Museum of Natural History.

## MATERIAL AVAILABLE

Approximately 200 bones are included in the avian collection from LACM locality 1945. Of these, 120 can be identified within four orders, and six families. At least 19 species are represented. Four of these, including a new genus, are herein described, making a total of five new species and two new genera typical of this locality (including *Praemancalla lagunensis* Howard, 1966). Four species are at least tentatively assigned to forms previously

described from other Tertiary localities in southern California. Others are identified only to family or genus.

For bibliographic reference to the related fossil species described from other areas, and the location of the types, the reader is referred to the Catalogue of Fossil Birds (Brodkorb, 1963, 1964, 1967). In addition to the LACM types listed, the LACM collections include casts of types of the following species: *Puffinus priscus, P. mitchelli, P. inceptor, P. conradi, P. diatomicus, Sula willetti, Miosula media, Palaeosula stocktoni, Morus lompocanus, Osteodontornis orri* and *Cerorhinca dubia.* These and referred LACM specimens of several extinct species from southern California Miocene and Pliocene localities were used for comparison, and are noted in the text. Where specimens or casts were not available, comparisons were based on the literature. Recent skeletons from the LACM collections were also used for comparison.

## LIST OF AVIAN SPECIES FROM LACM LOCALITY 1945

Order Procellariiformes
- Family Diomedeidae, albatrosses
  - *Diomedea* spp. (2 species)
- Family Procellariidae, shearwaters and fulmar
  - *Puffinus calhouni* n. sp.
  - *Puffinus priscus* Miller ?
  - *Puffinus* sp.
  - *Fulmarus hammeri* n. sp.

Order Pelecaniformes
- Family Pseudodontornithidae, extinct bony-toothed bird
  - *Osteodontornis orri* Howard ?
- Family Sulidae, boobies and gannets
  - *Microsula* sp.
  - *Morus lompocanus* (Miller) ?
  - *Miosula* ? sp.
  - Sulidae, sp.

Order Anseriformes
- Family Anatidae, geese
  - *Presbychen abavus* Wetmore
  - Anserinae, sp.

Order Charadriiformes
- Family Alcidae, auklets, etc.
  - *Alca* sp.
  - *Cerorhinca* sp.
  - *Aethia rossmoori* n. sp.
  - Alcidae, sp.
- Subfamily Mancallinae
  - *Alcodes ulnulus* n. gen. n. sp.
  - *Praemancalla lagunensis* Howard

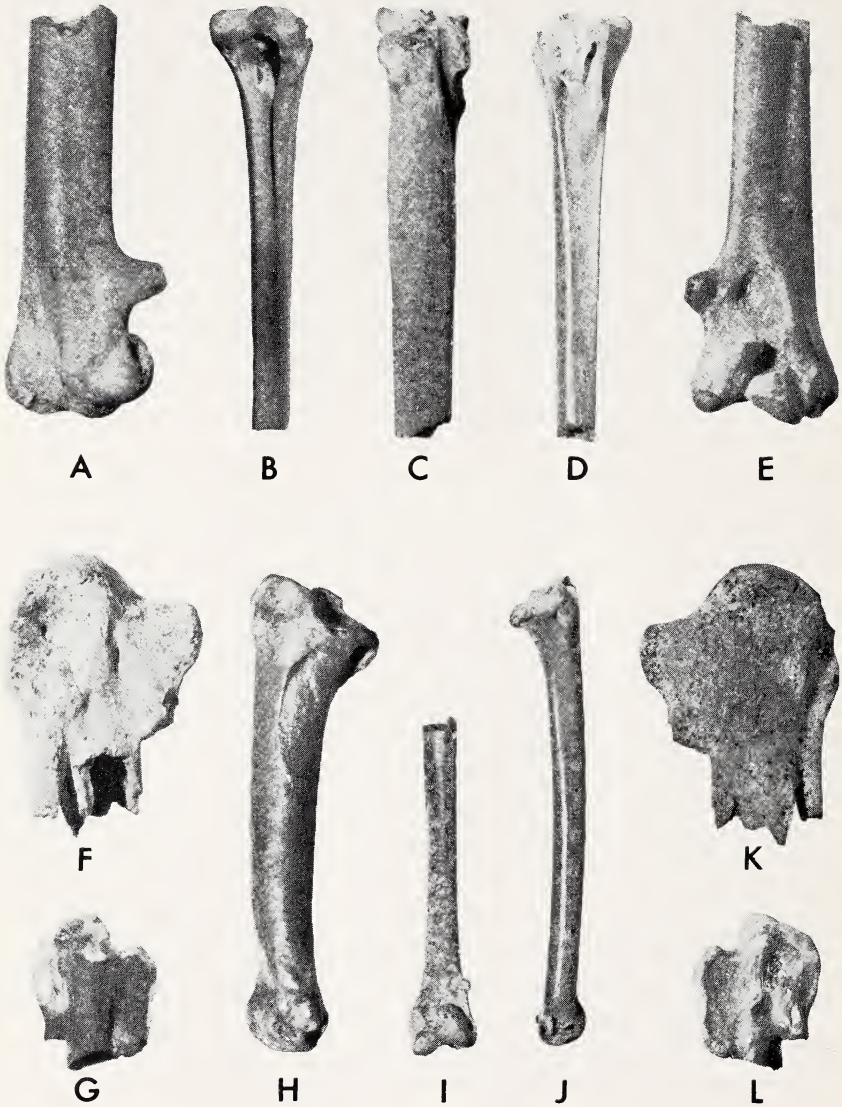


Figure 2. A-E *Puffinus calhouni* n. sp.; A and E, external and palmar views of type humerus; B, C, D, anterior, external and posterior views of referred tarsometatarsus (LACM 17582). F and K, internal and external views of type carpometacarpus of *Fulmarus hammeri* n. sp. G, H, L, *Alcodes ulnulus* n. sp.; G and L, external and internal views of referred carpometacarpus; H. internal view of type ulna. I-J, *Aethia rossmoori* n. sp.; I, referred humerus, palmar view; J, type ulna, internal view. All figures approximately X 2.

## ANNOTATED LIST OF SPECIES

### ORDER Procellariiformes

This order is the most abundantly represented. The 62 bones, assigned to two families and three genera, represent at least six species.

### FAMILY Diomedeidae

### GENUS **Diomedea** Linnaeus

### **Diomedea** spp.

A small fragment of the shaft of a tarsometatarsus near the proximal end (LACM 17550) is referred to the genus *Diomedea*. In size the specimen is similar to that element in *D. nigripes*, and is, therefore, too small to be assigned to *D. californica* Miller from the Miocene of Sharktooth Hill, and too large for *D. milleri* Howard from that same locality. There is little likelihood that the Recent *D. nigripes* is represented in a deposit of this age. The bone is too fragmentary to provide characters worthy of specific diagnosis.

A single pedal phalanx (LACM 18271), much larger than that of *D. nigripes*, and nearly equal in size to that of *D. exulans*, obviously represents a second fossil species, possibly assignable to *D. californica*.

### FAMILY Procellariidae

### GENUS **Puffinus** Brisson

Fifty-eight fragments are assigned to the genus *Puffinus*. The elements represented are: coracoid (4), scapula (3), humerus (9), ulna (14), radius (4), carpometacarpus (4), femur (1), tibiotarsus (3), tarsometatarsus (13), and one each of quadrate, cuneiform and wing phalanx.

Middle to Late Tertiary beds of southern California have already yielded six extinct species of *Puffinus*: *P. inceptor* Wetmore, *P. mitchelli* Miller and *P. priscus* Miller, all from the Middle Miocene of Sharktooth Hill; *P. diatomicus* Miller, from the Late Miocene diatomaceous shale of Lompoc; *P. felthami* Howard, from the Middle Pliocene of Corona del Mar; and *P. kanakoffi* Howard, from the Late Pliocene of San Diego.

Besides the California forms there are five species known from other North American and European deposits: *P. arvernensis* Milne-Edwards (Early Miocene of France), *P. micraulax* Brodkorb (Early Miocene of Florida), *P. aquitanicus* Milne-Edwards and *P. antiquus* Milne-Edwards (Middle Miocene of France), and *P. conradi* Marsh (Middle Miocene of Maryland).

The humerus (at least in part) is known in all of these species with the exception of *P. arvernensis*. The tarsometatarsus is known in *P. arvernensis, P. diatomicus, P. felthami* and *P. kanakoffi;* the ulna is tentatively recognized in *P. kanakoffi, P. mitchelli* and *P. priscus* (LACM coll. unrecorded). Several other elements of *P. kanakoffi* have been identified, and the proportions of some elements of *P. diatomicus* can be determined from skeletal impressions.

With a series of twelve Recent skeletons of *P. opisthomelas* as a basis of comparison, the various elements found in the present fossil collection and the incomplete skeletal representations for the other fossil species were assessed for possible similarities. It is clear that at least three species are present in the Laguna Hills material. One of these, new to science, is described here in honor of Mr. W. Earl Calhoun, who collected the type:

**Puffinus calhouni** n. sp.
Fig. 2, A-E

*Type*: Distal end of right humerus, LACM 17508; collected by W. Earl Calhoun, Jan. 18, 1965.

*Locality and Age*: LACM 1945, Leisure World, Laguna Hills, Orange County, California. Late Miocene?

*Diagnosis*: Humerus near the minimum in size range of humeri of *Puffinus opisthomelas;* impression of brachialis anticus muscle deep, more round than oval, and not extending proximally beyond upper level of ectepicondylar process; surface of attachment of anterior articular ligament shorter and broader than in *P. opisthomelas,* slightly convex and facing more palmad than laterad; external condyle narrow.

*Measurements*: Breadth of distal end, 7.1 mm; distance from distal end to proximal edge of ectepicondylar process, 9.3 mm; external depth of distal end, 6.5 mm; internal depth of distal end, 8.0 mm; dimensions of shaft, 3.0 (breadth) x 6.0 (depth) mm.

*Referred specimens*: Distal end of left humerus, LACM 17539; proximal end of right ulna, LACM 17530; proximal two-thirds of left tarsometatarsus, LACM 17582; all found on the same date as the type. An incomplete distal end of a humerus, LACM 17540, and two fragments of tarsometatarsal shafts, LACM 17524, with portions of hypotarsus present, are tentatively assigned.

Ulna 17530 is near the minimum in size range of ulnae of *P. opisthomelas.* Distinctions are as follows: attachment of anterior articular ligament narrow and oval (more crescent-shaped in *P. opisthomelas*), arising at edge of internal lip of cotyla without intervening depression, and terminating distally well below level of lip of external cotyla; brachial impression beginning distal to aforementioned ligamental attachment (not extending along the palmar side of the attachment); lip of external cotyla less abruptly set off from shaft, with a ridge connecting tip with shaft. Tarsometatarsus 17582 is heavier than that of *P. opisthomelas,* and further distinguishable by internal calcaneal ridge slightly mediad of internal surface of shaft; shaft deep externally, with anterior margin tending to curve mediad near proximal end. The tentatively assigned tarsometatarsi (LACM 17524) show the same mediad position of the internal calcaneal ridge and deep external side of shaft as in no. 17582, but the anterior margin is not so obviously incurved.

*Measurements of referred specimens*: Humerus 17539, breadth of distal

end, 7.1 mm; dimensions of shaft, 3.3 x 5.9 mm. Ulna 17530, breadth across proximal cotylae, 6.6 mm; depth from cotylae through olecranon, 7.7 mm; length of attachment of anterior articular ligament, 6.0 mm. Tarsometatarsus 17582, breadth of proximal end, 6.6 mm; breadth of shaft, 3.0 mm; depth of external side of shaft, 4.4 mm.

*Discussion*: Of the previously recorded fossil shearwaters, *P. diatomicus* most closely approaches *P. calhouni* in size. The humerus of *P. diatomicus* is immediately distinguishable, however, by the placement of the ectepicondylar process very high above the distal end, and proximal to the upper level of the impression of the brachialis anticus muscle. The tarsometatarsus of *P. diatomicus* resembles Laguna Hills specimen 17582 in the mediad position of the internal calcaneal ridge, but the internal contour of the proximal end is more flared proximally and laterally, resembling in this respect the condition in *P. griseus; P. calhouni* has the more symmetrical contours of *P. opisthomelas.* The characters of the humerus and tarsometatarsus of *P. diatomicus* are revealed in reverse casts made from the original skeletal impressions of the type and a referred specimen.

The humeri of *P. priscus* and *P. kanakoffi* are slightly broader than those of *P. calhouni,* and are distinguished further by the shallower impression of the brachialis anticus muscle, and a distinct pit at the lateral edge of the surface for the attachment of the anterior articular ligament; furthermore, in *P. priscus,* this surface faces more laterad than palmad. The distinction of *P. kanakoffi* is even more clearly shown in the tarsometatarsus, in which the hypotarsal region resembles that of *P. opisthomelas* in having the internal calcaneal ridge continuous with the internal border of the shaft, not inset mediad as in *P. calhouni.* The ulna of *P. kanakoffi* also resembles that of *P. opisthomelas.*

Six Miocene and Pliocene shearwaters are markedly larger than *P. calhouni* (*P. conradi, P. felthami, P. mitchelli, P. inceptor, P. antiquus, P. aquitanicus*); one is considerably smaller (*P. micraulax*). Although no measurements of *P. arvernensis* have been published, the tarsometatarsus, figured by Shufeldt (1896: pl. 24, figs. 1-2), appears to be much stockier than that of *P. calhouni.*

### **Puffinus priscus** Miller ?

A fragment of a distal end of a humerus (LACM 17548) is slightly larger than the humeri of *P. calhouni* and equals the type of *P. priscus* (7.5 mm) in breadth across the condyles. The bone is broken through the brachial impression below the ectepicondylar process. The only diagnostic character remaining is the attachment of the anterior articular ligament, which is flat and rotated laterally as in *P. priscus.* An incomplete proximal section of ulnar shaft (LACM 17547) suggests a larger bird than the ulna referred to *P. calhouni.* It is distinguished further by (1) a more prominent distal tip of the attachment of the anterior articular ligament, which terminates higher on the shaft than in

*P. calhouni,* and (2) the presence of a prominent papilla close to the base of the lip of the external condyle. The specimen closely resembles an ulna recently collected at Sharktooth Hill, which I am assigning to *P. priscus.*

A proximal end of tarsometatarsus (LACM 17538) resembles this element of *P. calhouni* in the medial inset of the internal calcaneal ridge, but posteriorly the external foramen is greatly enlarged and lies in a deep depression; the specimen is slightly heavier than those assigned to *P. calhouni,* and may represent *P. priscus.* No tarsometatarsi of shearwaters have yet been found at Sharktooth Hill, the type locality of *P. priscus.*

### **Puffinus** sp.

At least one additional species of shearwater is represented among the remaining specimens of *Puffinus.* An incomplete proximal end of a tarsometatarsus (LACM 17549), although similar in hypotarsal characters to *P. calhouni,* is distinctly larger (breadth of proximal end, 7.5 mm, approximately; breadth of shaft, 4.1 mm; depth of shaft, 5.0 mm). Of the larger North American fossil shearwaters, the tarsometatarsus is known only in *P. felthami.* The hypotarsal characters in *P. felthami* agree with those of Laguna Hills specimen 17549, but the shaft in the latter is deeper and heavier. A large distal end of tarsometatarsus (LACM 17523) from Laguna Hills may represent the same species as the proximal end. As the tarsometatarsus of *P. mitchelli, P. inceptor* and *P. conradi,* as well as those of the larger European species, cannot be compared, specific identification of these fragments is unwise.

The remaining 43 shearwater specimens in the collection probably belong either to *P. calhouni* or to the species tentatively identified here as *P. priscus.* Only a few of these are preserved in sufficient detail to present significant characteristics. Four incomplete coracoids (LACM 17528, 17529, 17531, 17534) are all broader through the triosseal canal than in Recent *P. opisthomelas,* the anterior (ventral) border below the furcular facet is straighter, and the furcular facet less pointed. All the coracoids are deeply concave through the triosseal canal, and in the three right ones a longitudinal groove, or trough, traverses the center of the area. In the left coracoid (LACM 17531) there is no central trough and the depressed area of the triosseal canal slopes directly to the anterior border. A single distal end of a femur (LACM 17516) is distinguished from that of *P. opisthomelas* in having a broader, deeper rotular groove (deeper, and broader than in *P. kanakoffi*).

### GENUS **Fulmarus** Stephens

Two poorly preserved specimens represent the fulmars, a proximal end of carpometacarpus and a fragment of the external side of the distal end of a humerus. The carpometacarpus of *Fulmarus* can be distinguished from that of *Puffinus* by the blunt, poorly developed pisiform process set posterior to the center of the internal face of the carpal area, and by the more rugose contour

of the external crest of the trochlea. The fulmar humerus is distinguishable from this element in the shearwaters by the longer, straighter palmar border on the external side below the ectepicondylar process, and the less distally developed external condyle with a broader, straighter anconal surface. The two Laguna Hills fragments resemble comparable elements of *Fulmarus glacialis,* but are larger. They are described as a distinct species named for Michael K. Hammer, who collected the type.

**Fulmarus hammeri,** n. sp.
Fig. 2, F, K

*Type*: Proximal end of left carpometacarpus, LACM 18262; collected by M. K. Hammer, Aug. 15, 1964.

*Locality and Age*: LACM 1945, Leisure World, Laguna Hills, Orange County, California. Late Miocene ?

*Diagnosis*: Closely resembling Recent *F. glacialis,* but approximately 20 per cent larger than the average of seven Recent specimens; process of metacarpal 1 relatively longer, and contour of external trochlear crest, posteriorly, at junction with metacarpal 3, smoother than in the Recent species.

*Referred specimen*: Distal fragment of external side of right humerus (LACM 18263) from the type locality, collected January, 1965. Similar to humeri of *F. glacialis,* but distinctly larger.

*Measurements*: Carpometacarpus, depth of proximal end from internal trochlear crest to tip of process of metacarpal 1, 13.1 mm (*F. glacialis* 10.1-11.2 mm, average 10.75); length of process of metacarpal 1, 8.8 mm (*F. glacialis* 6.1-7.0 mm; average 6.7 mm); breadth of trochlea, 5.5 mm approximately (*F. glacialis* 4.3-4.7 mm, average 4.5 mm). Humerus, distance from distal end to proximal edge of ectepicondylar process, 12.8 mm (*F. glacialis,* 10.6-11.6 mm, average 11.1 mm).

*Remarks*: The fossil carpometacarpus and humerus were not found together, but possibly some significance may be attached to the fact that both are among the few bones from locality 1945 that are of lighter color, and are seemingly somewhat less highly mineralized than most of the other specimens.

ORDER Pelecaniformes
SUBORDER Odontopterygia
FAMILY Pseudodontornithidae
Genus **Osteodontornis** Howard
**Osteodontornis orri** Howard ?

A fragment of a lower mandible (LACM 17557) bearing two bony tooth-like processes approximately 15 mm apart, with a small spine between them, represents an odontopterygiform bird. The specimen is narrower vertically than in the two known specimens of *Osteodontornis orri* (Howard, 1957; Howard and White, 1962), but possibly represents the extreme anterior end of

the jaw, which has not been clearly determined in the other specimens. The "tooth" processes measure 6.8 mm and 4.8 mm, respectively, across their bases. The smaller of the two is as tall as long and although slightly water worn, its pointed tip suggests that its height is nearly complete. The larger "tooth" is blunt and eroded, with a possible height of 8 mm or more. Neither "tooth" equals in size the major projections in the mandible of the type of *O. orri,* nor in that of the related *Pseudodontornis longirostris* (Spulski), whose origin and age are unknown. The tentative assignment to *Osteodontornis orri* is based on the previous records of the species as the only representative of the group from southern California.

## SUBORDER Sulae
## FAMILY Sulidae

Twenty-seven fragments are assignable to the Sulidae. The following elements are represented: coracoid (1), scapula (3), humerus (2), radius (5), carpometacarpus (6), femur (1), tibiotarsus (1), tarsometatarsus (3), quadrate (2), cuneiform (1), pedal phalanx (1) and sacral fragment (1). At least three species are represented by the five radii, and a fourth, and smaller, species is indicated by one of the humeri. The other specimens are tentatively grouped within these four species. None of the species can be definitely named.

Eight middle and late Tertiary species of sulids have been recorded from southern California: *Sula willetti* Miller, *S. pohli* Howard, *Morus vagabundus* Wetmore, *M. lompocanus* (Miller), *Miosula media* Miller and *Palaeosula stocktoni* (Miller) from the Miocene; *Sula humeralis* Miller and Bowman and *Miosula recentior* Howard from the Pliocene. Four are known from Florida: *Sula universitatis* Brodkorb, Miocene; *Sula guano* Brodkorb, *S. phosphata* Brodkorb and *Morus peninsularis* Brodkorb, Pliocene. Two are recorded from the Maryland Miocene: *Microsula avita* (Wetmore) and *Morus loxostylus* (Cope); the latter is also recorded from New Jersey. One species, *Microsula pygmaea* (Milne-Edwards), is recorded from the Miocene of France.

For the most part, the same elements cannot be compared between the Laguna Hills assemblage and the material from other localities. It would, therefore, serve only to confuse the record to attempt definite assignment of these fragmentary specimens. It is hoped that as more Tertiary bones become available, it will be possible to make a detailed analysis of the group. Such an analysis may well result in a revision of current generic usage among the fossils. The skeletal characters that separate *Morus* and *Sula* among living birds are not always distinct in the fossils, and do not hold true in all comparable elements.

### GENUS **Microsula** Wetmore
### **Microsula** sp.

A small humerus (LACM 17556) agrees in size with the type of *Micro-*

*sula avita* (Wetmore) and further conforms to Wetmore's (1938:22-23) description as follows: ectepicondylar process slight, internal condyle globular and projecting distinctly distal to the level of the external condyle, brachial impression slightly depressed, attachment of anterior articular ligament short and broad. The specimen differs from that of *M. avita,* however, as follows: olecranal fossa deeper and more round than oval, surface for attachment of anterior articular ligament as broad distally as it is proximally (Wetmore's illustration of *M. avita* shows this surface to narrow distally), and brachial impression more deeply depressed in its distal than in its proximal half.

A distal half of a carpometacarpus (LACM 17555) agrees with Wetmore's illustration (*op. cit.,* fig. 3) of this element assigned to *Microsula avita* in the shortness of the distal symphysis and the absence of pneumatic foramina. This fragment cannot be distinguished from the carpometacarpus assigned to *M. avita* by Wetmore. *Microsula* is characterized by the reduction of pneumaticity in comparison with living members of the family Sulidae, as observed primarily in the carpometacarpus, but presumably noted in the humerus as well. The Laguna Hills humerus has only one small pneumatic foramen in the olecranal fossa.

A small proximal end of a tarsometatarsus (LACM 17554) is possibly assignable to the same species as the humerus and carpometacarpus, but presumably to a slightly larger individual. The shaft has a narrow, deep excavation anteriorly, with heavy, rounded margins. The two foramina above the large, oval tubercle for the tibialis anticus muscle are inconspicuous and appear to be the only openings in the area, suggesting the reduced pneumaticity which characterizes the other elements. The intercotylar tuberosity is prominent as in *Sula,* as contrasted with *Morus.* The relationship between the middle and internal calcaneal ridges is closer to the condition found in *Sula,* although the posterior surface of the internal ridge has less medial extent.

The humerus (LACM 17556) indicates that the Laguna Hills species is not *Microsula avita.* From Wetmore's statement (1938:23) regarding the distinction of *M. pygmaea* from *M. avita* (smaller size and different confirmation of ectepicondylar area), it seems safe to assume that this distinction extends, as well, to the Laguna Hills specimen. The only other previously described sulid that could have been as small as the species here represented is *Sula willetti. S. willetti* is recorded from three Tertiary localities in southern California, all presumably of Late Miocene age. The possibility that the Laguna Hills specimens could be assignable to *S. willetti* cannot be overlooked. It should be noted that *Microsula* was originally established (Wetmore 1938:25) as a subgenus of *Sula,* characterized only by reduced pneumaticity of the bones. The characteristics of *S. willetti* that link it with *Sula* as contrasted with *Morus* do not rule out the possibility of relationship to *Microsula.* One characteristic of *S. willetti* that is not true of Recent *Sula* is the shortness of the ulna in proportion to the humerus. The presence or absence of pneumatic foramina,

and other details of individual elements cannot be determined from the impressions that provide the only records of *S. willetti.*

### GENUS **Morus** Viellot
### **Morus lompocanus** (Miller) ?

A well preserved distal end of a tibiotarsus (LACM 17570) has the relatively great anteroposterior depth that characterizes this element of *Morus* as distinguished from the broad, flat tibiotarsus of *Sula.* The fossil is larger in all dimensions than that of the only available Recent skeleton of *Morus bassanus.* The size suggests the possibility of allocation to *M. lompocanus,* known to be a bird of large size, although the tibiotarsus itself cannot be compared. The tibiotarsus of *Miosula media* Miller, which can be seen on a reverse cast of the type, is also of large size. Both this specimen, and the type of *Miosula recentior,* however, have greater lateral and distal thrust of the external condyle than in *Morus* and the specimen from Laguna Hills.

Two proximal ends of radii (LACM 17574 and LACM 18268) resemble *Morus* more closely than *Sula* in this element, but do not quite equal the dimensions of the radius of *M. bassanus* at hand. Their relationship to the tibiotarsus is questionable.

### GENUS **Miosula** Miller
### **Miosula** ? sp.

Nine specimens are water worn fragments that have adhering to them a highly indurated matrix distinctly different from the embedding sands from which the specimens were recovered. It is suggested that the bones may have been washed into the sands from an earlier deposit. The preservation is very poor, the water worn contours and hard matrix (that defies removal, and is itself water worn) obscuring many of the diagnostic characters. Elements represented are: coracoid (LACM 17569), radius (LACM 17568), carpometacarpi (LACM 17566 and 17579), tarsometatarsus (LACM 17565), femur (LACM 18269), two unnumbered quadrates and a sacrum. The coracoid, radius, proximal end of carpometacarpus (LACM 17566), and tarsometatarsus show some significant features.

The coracoid is worn along the external edge of the head so as to disguise the true contours in this area. Characters of the triosseal canal, scapular facet and ligamental attachment on the antero-internal side of the head resemble the coracoid of *Sula* as distinguished from that of *Morus.* In breadth across the triosseal area, it slightly exceeds this element in a Recent female adult specimen of *Sula dactylatra,* and is therefore, notably larger than any of the Miocene or Pliocene fossil species described in the genus *Sula.*

The proximal end of carpometacarpus (LACM 17566) is slightly smaller than in the Recent specimen of *S. dactylatra.* It differs from this element of both *Sula* and *Morus* in closer proximity of attachment of metacarpal 3 to the

trochlea, greater posterior curvature of metacarpal 3, and absence of pneumatic foramina. Pneumatic foramina are fewer in *Morus* than in *Sula,* and there is a slight tendency to posterior curvature of metacarpal 3 in *M. bassanus.* A somewhat closer similarity of the fossil to *Morus* than to *Sula* is, therefore, suggested.

The distal fragment of radius (LACM 17568) is also smaller than in *S. dactylatra* and bears distinctive characters that could be of generic significance. In angularity of the distal contour, the resemblance is closer to radii of *Sula* than of *Morus,* but differences are clearly marked. The ligamental prominence is more swollen, the shaft is relatively deeper and narrower, and the external contour of the shaft above the articular facet curves in abruptly and lacks the flangelike marginal projection found in *Sula.* Most distinctive, however, is a large, deep, oval depression centrally located, the abrupt margins of which, as well as its depth, suggest pneumaticity; actual openings, if present, are obscured by the hard, adhering matrix. The specimen is clearly distinct from the two distal ends of radii listed below under Sulidae sp., and its smaller size sets it apart from those represented by proximal ends tentatively allocated to *Morus lompocanus.*

The tarsometatarsus, a proximal half, has a relatively narrow shaft as in *Morus,* with a lateral dimension (taken immediately below the internal calcaneal ridge) approximately that of the tarsometatarsus of *M. bassanus* (narrower than that of *S. dactylatra*), but with a depth on the internal side at the same point on the shaft, 2 mm greater than in *M. bassanus.* Detailed contours of the proximal end are incomplete; the anterior portion is broken away so that the degree of prominence of the intercotylar tuberosity cannot be determined. Posteriorly, the position of the innermost calcaneal ridge is more medial with respect to the internal cotyla than in *Morus* (closer to *Sula*) and the second ridge is more definitely bridged to the first (also closer to *Sula*).

Because of the distinctive preservation of the nine bones, one is tempted to think of them as belonging to one species even though they were not actually associated. At least three of the elements (carpometacarpus, radius, tarsometatarsus) appear to be generically distinct from both *Sula* and *Morus.* The proportions of large coracoid and tarsometatarsus with relatively smaller radius and carpometacarpus suggest the possibility that *Miosula* may be the genus represented. The genotype of *Miosula, M. media* Miller (1925:115), is characterized by these proportions. The type of *M. media* is a skeletal impression in which only the tarsometatarsus can be compared with the Laguna Hills bones. This element from the two localities is the same in overall size and slender proportions. Unfortunately the details of the anterior side of the proximal end, which show in *M. media,* are lacking in the Laguna Hills bone, and characters of the posterior side are obscured in the matrix in the type of *M. media.*

Sulidae, sp.

Two distal ends of radii (LACM 17572 and 18264) differ from specimen no. 17568, tentatively assigned to *Miosula*. They differ also from Recent speciments of this element in *Morus* and *Sula* in the absence of pneumatic foramina; and in other particulars, as well, do not exactly conform to either of the Recent genera. The smoothness of the ulnar depression and the slight development of the ligamental prominence more nearly resemble the condition in *Morus* than in *Sula*. But there is less flare of the distal end, and the ulnar side of the shaft has a markedly angular apex extending to the distal facet. Although it is difficult to take exact measurements on these fossil specimens, they seem to fall within the size range of radii of *Sula leucogaster brewsteri*, and are distinctly smaller than those tentatively listed above under *M. lompocanus*, but too large to be assigned to *Microsula*. A complete cuneiform (LACM 17562), a fragment of an articular end of a scapula (LACM 17560), and a middle trochlea of tarsometatarsus (LACM 17575) all show characters closer to those of comparable elements of *Morus* than of *Sula*, but their fragmentary condition does not permit of definite allocation. All are notably smaller than comparable elements of *M. bassanus*, and only slightly larger than the maximum of four specimens of *S. leucogaster brewsteri*.

Three distal fragments of carpometacarpi (LACM 17558, 17561 and 17578) lack foramina in the distal symphysis, and thus differ from both *Sula* and *Morus*. They slightly exceed the maximum of *S. leucogaster brewsteri* in size.

ORDER Anseriformes
FAMILY Anatidae
GENUS **Presbychen** Wetmore
**Presbychen abavus** Wetmore

A fragment of the proximal end of a tarsometatarsus (LACM 17552) agrees in size with, and resembles in the qualitative characters preserved, the tarsometatarsus from Sharktooth Hill assigned to *Presbychen abavus* (Howard, 1966b:8). The characters are as follows: anterior face of shaft deeply depressed in region of proximal foramina, flattening toward internal side through area of attachment of tibialis anticus muscle, but internal border retaining a distinct ridge for a slightly greater distance distally than in the Sharktooth Hill specimen; external surface of shaft deep anteroposteriorly. Exact measurements cannot be made.

A femur (LACM 17553) also agrees, in such characters as are preserved, with the femur from Sharktooth Hill assigned tentatively to *P. abavus* (Howard, 1966b). Both femora are very poorly preserved and can be analyzed only in the most general manner: head large, upturned, neck well defined; greatest lateral extent of external contour of articular end nearly central with respect to anteroposterior dimensions, anterior edge of trochanter seemingly blunt,

lacking curved, pointed tip. The only accurate measurement possible is the anteroposterior dimension through the trochanteric crest, 16.6 mm. This is approximately 10 per cent less than in minimum specimens of *Cygnus olor* or *Olor columbianus.*

A scapula (LACM 17551) of a large anserine is also assigned to *Presbychen,* although specific allocation to *P. abavus* is doubtful as the specimen does not exceed this element of *Branta canadensis* in size. The scapula resembles this element in *Cygnus,* and is distinguished from that of *Branta,* or any other living goose, in the absence of a dorsal pneumatic foramen. It differs from the extinct *Eremochen,* in which the foramen is absent, in having a large, knoblike coracoidal tuberosity (suggestive of the condition in *Cygnus*) and a raised area in the posterodorsal region where the foramen would be. Cygnine characters have also been noted in the tarsometatarsus from Sharktooth Hill assigned to *P. abavus* (Howard, 1966b).

Anserinae, sp.

A distal end of a radius (LACM 18270) represents a small goose, no larger than *Branta nigricans.*

ORDER Charadriiformes
FAMILY Alcidae

Except for the flightless, mancallid auks, which are now recognized as a subfamily of the Alcidae (Brodkorb, 1967), the alcids are rare in the California fossil record. A single specimen, described as *Cerorhinca dubia* Miller, occurred in the Lompoc Miocene, and *Brachyramphus pliocenus* Howard and *Ptychoramphus tenuis* Miller and Bowman were described from the Pliocene of San Diego. Elsewhere in the United States records include *Miocepphus mcclungi* Wetmore (Maryland Miocene), *Uria antiqua* Marsh (North Carolina Miocene) and *Australca grandis* Brodkorb (Florida Pliocene). A single Pliocene species, *Uria ansonia* Portis, is recorded from Europe (Italy). The mancallids (*Mancalla californiensis* Lucas and *M. diegense* (Miller)) occur in several Pliocene sites in California and are represented in the locality here under discussion by the species *Praemancalla lagunensis* Howard.

Besides the six bones of *P. lagunensis* previously recorded (Howard, 1966a), an additional 21 specimens of auklike birds are present in the collection from LACM locality 1945. The following elements are included: coracoid (6), humerus (3), ulna (7), radius (1), carpometacarpus (2), and tarsometatarsus (2). None is well preserved, but 12 show sufficiently diagnostic characters to be referred to two new species. The others seemingly represent another three or four species, but cannot be definitely assigned.

GENUS **Alca** Linnaeus
**Alca** sp.

A fragment of a right coracoid (LACM 18282) lacks the head and the

tip of the procoracoid, and is broken just below the connection of the procoracoid to the shaft. It closely resembles this element in *Alca torda* in development of the procoracoid and clearly defined coracoidal foramen, but is of slightly smaller size. It would be unwise to attempt description on so incomplete a fragment.

Humerus LACM 18283, which lacks the proximal end, resembles the humerus of *Alca torda* most closely in the tricipital grooves and the curvature of the anconal contour of the shaft near the distal end. The distal end is worn and incomplete, but the attachment of the anterior articular ligament appears to have been more projecting and more palmad in direction than in the Recent species. The bone is both shorter and stouter than the humerus of *A. torda.*

## GENUS **Cerorhinca** Bonaparte

### **Cerorhinca** sp.

A proximal end of an ulna (LACM 18274) resembles this element of *Cerorhinca monocerata* in conformation, with a narrow, rather depressed brachial impression undercutting the prominence for the anterior articular ligament, and with a short olecranon. Each of these characters is, however, exaggerated in the fossil, and the size of the bone indicates that it represents a species of smaller size than *C. monocerata.* The Miocene *Cerorhinca dubia,* known only from the impression of the leg bones, was probably a bird of about the same size.

A small fragment of a shaft of humerus (LACM 18275) near the distal end may represent the same species.

## GENUS **Aethia** Merrem

A complete ulna of very small size resembles this element in *Aethia* in the blunt olecranon and the small, basinlike depression between the olecranon and the external cotyla, delimited by a definite ridge externally. Other characters, however, distinguish the fossil ulna from the comparable element in living species of *Aethia,* and indicate that it represents an extinct form. This is the first fossil record of the genus. In naming the species, I take pleasure in honoring Mr. Ross Cortese who developed the senior citizen community at Laguna Hills under the name of Rossmoor Leisure World.

### **Aethia rossmoori** n. sp.

Fig. 2, I, J

*Type*: Right ulna complete except for tip of olecranon; LACM no. 18948; collected by LACM party, Aug. 15, 1964.

*Locality and Age*: LACM 1945, Leisure World, Laguna Hills, Orange County, California. Late Miocene ?

*Diagnosis*: Close to *Aethia pusilla* in size, but shaft of ulna rounder, less bladelike; attachment of anterior articular ligament more prominently projected laterally; olecranon broken at tip, but seemingly even less developed than in *A. pusilla*; external crest of trochlea slightly less developed both proximally and in depth; carpal tuberosity prominent and forming a hook.

*Measurements*: Greatest length, 28.0 mm; least breadth of shaft, 1.7 mm; least depth of shaft, 2.0 mm; breadth across proximal cotylae, 3.9 mm; greatest breadth of distal end through carpal tuberosity, 3.1 mm; depth of external crest of distal trochlea, 3.2 mm.

*Referred specimen*: Left humerus, LACM no. 18949, collected on the same day as the type. The specimen resembles that of *Aethia pusilla* in the papillalike process at the proximal tip of an otherwise poorly developed ectepicondylar process. The shaft is even more rounded than *A. pusilla* and the attachment for the anterior articular ligament faces even more directly palmad than in the living species. Measurements: breadth of distal end, 4.1 mm; breadth and depth of shaft above ectepicondylar process, 2.5 mm in each dimension; least breadth of shaft, 1.8 mm, depth of shaft at same place, 2.3 mm.

*Tentatively referred specimens*: Distal half of ulna, LACM 18960, similar to type except carpal tuberosity seemingly less hooked. Proximal half of radius (LACM 18953) and distal half of carpometacarpus (LACM 18951) both of appropriate size, but too fragmentary for analysis.

Three fragmentary coracoids (LACM 18952 and 18954 (two)), all lacking the head, represent an auklet of the same small size as the other specimens. All differ from Recent individuals of *Aethia* in the more distally extended procoracoid, pierced by a clearly defined foramen. One character which distinguishes them from those Recent genera of alcids in which the procoracoid is well developed and the foramen present, is the position of the procoracoid and the glenoid facet in relation to the shaft. The fossils resemble *Aethia* in that the procoracoid arises at the internal edge of the shaft, and the glenoid facet faces posteriorly; in the Recent genera that have a foramen, the procoracoid arises slightly posterior to the internal border of the shaft, and the glenoid facet faces more externally, not directly posteriorly.

## Alcidae, spp.

Five fragments cannot be generically assigned. Two coracoids (LACM 18276) appear to have a short procoracoid, either notched, as in some individuals of *Cepphus,* or lacking a foramen entirely, thus differing from LACM 18282 assigned to *Alca.* The size is about that of the pigeon guillemot, *Cepphus columba.* Both specimens lack the head.

A proximal portion of an ulna (LACM 18272) lacks the olecranon, and is badly eroded through the cotylae. It is distinctive in having a relatively broader brachial impression than in any Recent genus. The shaft depth is close to this dimension in *A. torda,* but the breadth is considerably greater. The

attachment of the anterior articular ligament is prominent and convex, and is undercut by the brachial impression along its palmar edge.

Two tarsometatarsal fragments (LACM 18273 and 18281) are close in size to tarsometatarsi of *Uria aalge,* but are too incomplete for identification.

Size alone suggests that at least two species are represented by these specimens. The coracoids suggest a bird close in size to *Cepphus columba.* The tarsometatarsi and ulna represent a larger form (or forms?).

SUBFAMILY Mancallinae
NEW GENUS **Alcodes**

*Type Species*: *Alcodes ulnulus,* n. sp. (*Alca,* auk; *odes,* similar to; *ulnulus,* small ulna).

*Diagnosis*: Ulna relatively short, with proximal breadth 18 per cent of length, and proximal depth 24 per cent of length; brachial impression well defined, its length 2 per cent greater than depth of proximal end, its breadth 39 percent of its length; contours of ligamental attachments and olecranon blunt. Carpometacarpus with anterior border of process of metacarpal 1 nearly straight; length of process 91 per cent of depth of proximal end; facet for phalanx 1 slightly distal to proximal symphysis; trochlea nearly flat across proximo-anterior surface, and narrowing posterodistally.

**Alcodes ulnulus** n. sp.
Fig. 2, G, H, L

*Type*: Complete left ulna, LACM 18277, collected by W. Earl Calhoun, December 24, 1964.

*Locality and Age*: LACM 1945, Leisure World, Laguna Hills, Orange County, California. Late Miocene ?

*Diagnosis*: See Generic Diagnosis.

*Description*: Ulna short and stocky with proximal and distal ends laterally compressed; shaft rounded on internal surface, tapering slightly in depth distal to center; olecranon deep but blunt; brachial impression short and broad, bordered towards its proximal end by the smoothly rounded prominence for attachment of the anterior articular ligament; markings for feather attachments clearly visible externally as six slightly raised papillae near anconal ridge, and as seven small depressions towards center of external surface of shaft; carpal tuberosity heavy and blunt, not projecting; lip of external cotyla blunt in palmar contour.

*Measurements*: Greatest length, 30.9 mm; breadth of proximal end, 5.7 mm; depth of proximal end through olecranon, 7.5 mm; depth of external side of distal trochlea, 5.4 mm; breadth across distal trochlea, 3.8 mm; length of brachial impression, 7.7 mm; greatest breadth of brachial impression, 3.0 mm; depth of shaft at distal tip of brachial impression, 4.5 mm, breadth of shaft at same place, 2.9 mm.

*Referred material*: Distal end of right ulna (LACM 18279); proximal

end of right carpometacarpus (LACM 18278); and, tentatively, proximal portion of right ulna lacking olecranon and complete contours of cotylae (LACM 18280). All specimens were collected at the type locality in December, 1964.

The distal end of ulna is so similar to the type that it could represent the same individual. The incomplete proximal half of ulna resembles the type in the short, broad brachial impression, placement of feather attachments and shape of shaft, but is at least 10 per cent larger than the type.

The carpometacarpus seemingly represents an individual of the same size as the type. Characters are as follows: process of metacarpal 1 elongated, proximo-distally with facet for phalanx 1 distal to proximal symphysis, and small in size; anterior border of process nearly straight; external crest of trochlea less proximally extended than in Recent alcids; distal tip of internal crest of trochlea merging into metacarpal 3 without marked notch; trochlea nearly flat across proximo-anterior surface, narrowing posteriorly; distal lobe of external crest greatly reduced, metacarpal 3 aligned with distal edge of internal crest of trochlea; pisiform process small. Measurements of carpometacarpus: breadth of trochlea, 3.8 mm; depth of proximal end through internal crest of trochlea and process of metacarpal 1, 8.0 mm; length of process of metacarpal 1, 7.3 mm.

*Discussion*: The proportions of the type ulna of *Alcodes ulnulus* are distinctive. The proximal breadth is greater than in *Ptychoramphus aleuticus,* the proximal depth approaches that of *Cepphus columba.* But the length of the element falls far short of either species and more closely approximates that of the tiny Least Auklet, *Aethia pusilla.* The short, stocky bone suggests that *A. ulnulus* was progressing towards flightlessness. Such proportions of the ulna are not to be found in any living alcids. However, the ulna does not have the paddlelike proportions of the flightless *Mancalla,* or even *Pinguinis,* or its possible forerunner, *Australca grandis.*

The carpometacarpus also reflects the trend toward flightlessness. The elongated process of metacarpal 1, the smooth surface of the trochlea and reduction of the trochlear crests suggest a tendency towards the condition found in *Praemancalla,* but with less modification. As previously noted (Howard, 1966a), *Praemancalla* was less advanced in development of the paddlelike wing than *Mancalla.* On the basis of the characters of the carpometacarpus, *Alcodes* shows closer relationship to the mancallids than to the true alcids (see Howard, 1966a:3). However, characters of both the carpometacarpus and the ulna suggest a collateral, rather than a direct line with respect to *Praemancalla* and *Mancalla.*

### **Praemancalla lagunensis** Howard

The six specimens of this extinct species from LACM locality 1945 were all discussed in the type description (Howard, 1966a). The elements included are humerus, coracoid, carpometacarpus (2), scapula and fragment of lower mandible.

## SUMMARY AND CONCLUSIONS

The 19 or more avian species from Laguna Hills locality LACM 1945 comprise a marine avifauna in which the Family Procellariidae predominates in number of specimens (60). The Sulidae and the Alcidae, each with 27, are next in abundance. Scant representation of the Anatidae (4), Diomedeidae (2) and Pseudodontornithidae (1) complete the total identified avifauna.

Although in its entirety the avifauna does not relate to that of any one previously recorded locality, the forms included show closer resemblance to those of the Miocene rather than to those of the Pliocene. None of the species recorded from the marine Pliocene of Orange and San Diego counties is even tentatively recognized in the material from LACM locality 1945. On the contrary, the typical Pliocene genus of flightless auks, *Mancalla,* so abundantly represented in the San Diego deposits, and present, also, in the Corona del Mar beds and localities 65120 and 65121 of Leisure World, Orange County, is absent in the LACM 1945 avifauna and the Mancallids are represented by the related, but less highly specialized, genus *Praemancalla.*

Several identifications (*Morus lompocanus* ?, *Miosula* ? sp., and *Cerorhinca* sp.) suggest similarity with species from the Late Miocene Lompoc diatomite, but because of the great difference in preservation of material from the two localities, no definite identifications can be made. The possibility that *Sula willetti,* also described from the Lompoc beds, might be represented by the fragments here referred to *Microsula* sp. is noted. The most abundant species of Lompoc, *Puffinus diatomicus,* is, however, absent.

One species, *Presbychen abavus,* previously recorded only from the Sharktooth Hill Middle Miocene, is identified, and one of the shearwaters of that locality, *Puffinus priscus,* is tentatively recognized. However, the sulid representation of locality 1945 does not include, even tentatively, the most abundant species of the Sharktooth avifauna, *Morus vagabundus.* The bony-toothed bird, *Osteodontornis orri,* heretofore recorded from both Middle and Late Miocene in southern California, is tentatively listed in the Laguna Hills avifauna.

The avifauna as a whole corroborates the evidence afforded by the primitive *Praemancalla* (Howard, 1966a:8), indicating a Miocene (probably Late Miocene) age of deposition of the fossil-bearing strata at LACM locality 1945, Laguna Hills.

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# A NEW PICULET FROM AMAZONIAN BOLIVIA

*By* KENNETH E. STAGER

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DOROTHY M. HALMOS
*Editor*

# A NEW PICULET FROM AMAZONIAN BOLIVIA

*By* Kenneth E. Stager[1]

Abstract: A new race of *Picumnus rufiventris* from Todos Santos, central Bolivia is described and named *Picumnus rufiventris brunneifrons*. The relationships of *P. r. brunneifrons* with the nominate race *P. r. rufiventris* of Colombia and Ecuador and the large race *P. r. grandis* of Peru and Brazil are discussed.

During a revisional study of the neotropical pygmy woodpeckers of the genus *Picumnus*, an undescribed subspecies of *Picumnus rufiventris* has been found and, in anticipation of the complete revision of this genus, is named as follows:

**Picumnus rufiventris brunneifrons,** new subspecies

*Type*: Adult male, collected at Todos Santos, Rio Chaparé, Dept. Cochabamba, Bolivia, at an altitude of 1000 feet (300 m), September 7, 1937, by M. A. Carriker, Jr., ANSP 143390.

*Diagnosis*: Similar to *Picumnus r. grandis* (Carriker, 1930), but smaller, darker and with the feathers of the forehead a distinctive brown instead of black.

*Description of Type*: (Capitalized color terms are those of Ridgway, 1912.) Crown and nape deep black with each feather tipped with white or Nopal Red. The red tipping is restricted to the center of the crown and nape. The feathers of the nape are broadly tipped with Nopal Red, with the amount of red decreasing anteriorly on the crown. The lateral feathers of the crown are tipped with round spots of white. The feathers of the forehead are uniformly Snuff Brown, but each with a subterminal tip of black and a smaller terminal tip of white. Entire back, rump and shoulders Yellowish Olive. Sides of throat, cheeks and a broad dorsal neck band (8 mm) warm Argus Brown; center of throat, chest, abdomen and flanks rich Amber Brown; primaries, secondaries and tertials Fuscous Brown; outer edge of secondaries and coverts Yellowish Olive; tail coverts Amber Brown; tail black with the middle pair of rectrices Sayal Brown on the inner webs and distal portion of outer webs; the two outer pairs having a broad band of the same color running obliquely across the basal portion of the outer web to the subapical portion of the inner web; under wing coverts and axillaries Amber Brown. Wing, 58.0 mm; tail, 31.0 mm; culmen, 17 mm.

*Measurements*: Adult males (5), wing 57.0-61.5 mm (average 58.5 mm); tail 28.5-32.0 mm (average 30.5 mm); culmen 15.3-18.5 mm (average 17.3 mm). Adult females (6), wing 58.0-61.0 mm (average 59.7 mm); tail 30.0-

[1]Senior Curator of Ornithology, Los Angeles County Museum of Natural History.

33.0 mm (average 31.3 mm); culmen 16.4-17.0 mm (average 16.9 mm). Immature female (AMNH), wing 58.5 mm, tail 31.0 mm, culmen 15.5 mm.

*Range*: Known only from a series of 12 specimens, 11 of which are from the type locality and one (LSU) from the Rio Mamoré, Dept. Beni, Bolivia.

*Remarks*: *Picumnus rufiventris brunneifrons* of Bolivia is the southeasterly race of the rufous-breasted piculet that ranges from eastern Colombia and Ecuador (*P. r. rufiventris*), through eastern Peru and western Brazil (*P. r. grandis*). The nominate race and *P. r. brunneifrons* are somewhat similar in size, but are widely separated geographically by the larger sized race *P. r. grandis*. A hiatus of nearly 600 direct line miles separates the most southeasterly locality known for *P. r. grandis* (mouth of the Rio Inambari, Peru) from the type locality of *P. r. brunneifrons* in central Bolivia (Todos Santos).

A comparison of the male pileum in all three subspecies shows the foreheads of both *P. r. grandis* and *P. r. brunneifrons* to be heavily dotted with white, while the forehead of *P. r. rufiventris* is characterized by an almost total absence of white dots. The females of *P. r. brunneifrons* are identical to the males in color pattern except for the absence of the red tipping to the feathers of the crown, the red being replaced with round white dots. *Picumnus r. brunneifrons* is immediately separable from the other two subspecies by the presence of the distinctive brown forehead in both males and females.

*Specimens Examined*: Academy of Natural Sciences of Philadelphia (ANSP), 5 (2 ♂♂, 3 ♀♀) Todos Santos, Department of Cochabamba, Bolivia; American Museum of Natural History (AMNH), 2 (2 ♀♀) Todos Santos, Department of Cochabamba, Bolivia; Paris Museum (PM), 2 (1 ♂, 1 ♀) Todos Santos, Department of Cochabamba, Bolivia; Louisiana State University (LSU), 3 (2 ♂♂, 1 ♀) Todos Santos, Department of Cochabamba and Rio Mamoré, Department of Beni, Bolivia.

For the loan of comparative material of *rufiventris*, I am indebted to the American Museum of Natural History; the Academy of Natural Sciences of Philadelphia; the Museum of Comparative Zoology; the Louisiana State University; the Field Museum; the Museum of Zoology, University of Michigan; and the Moore Laboratory of Zoology, Occidental College.

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# STUDIES ON NORTH AMERICAN BEES OF THE GENUS *HYLAEUS*. 4. THE SUBGENERA *CEPHALYLAEUS*, *METZIELLA* AND *HYLAEANA* (Hymenoptera: Colletidae)

*By* ROY R. SNELLING

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# STUDIES ON NORTH AMERICAN BEES OF THE GENUS *HYLAEUS*. 4. THE SUBGENERA *CEPHALYLAEUS*, *METZIELLA* AND *HYLAEANA*

(Hymenoptera: Colletidae)

*By* Roy R. Snelling[1]

Abstract: In this paper representatives of the subgenera *Cephalylaeus, Metziella* and *Hylaeana* are considered. Keys to the forms allocated to each subgenus are presented to distinguish the specific populations. Data concerning the distribution of each species are given.

This is the fourth in a series of studies contributing toward a monograph of the North American *Hylaeus*. The previous parts have appeared as indicated in the literature cited (Snelling, 1966a, b, c). The three subgenera included in the present study may be recognized by the characters indicated in Part 3 (Snelling, 1966c).

## Key to Species of *CEPHALYLAEUS*

1. Males ..... 2
   Females ..... 3

2. Clypeus 1.3 times as long as broad, not greatly protuberant, tesselate between punctures; punctures of first tergite moderately coarse, separated by a puncture diameter or less; integument dull, strongly tesselate ..... *basalis* (F. Smith)

   Clypeus slightly broader than long, strongly and abruptly protuberant, shiny, interspaces between punctures slightly tesselate; punctures of first tergite fine, separated by more than a puncture diameter; integument between punctures moderately shiny, weakly tesselate ..... *nunenmacheri* Bridwell

3. Propodeum without distinctly horizontal basal area, evenly sloping toward apex, basal area with rugulae confined to extreme base; supraclypeal area with a number of large punctures; mesopleura shiny between well-separated punctures ..... *nunenmacheri* Bridwell

   Propodeum with distinctly horizontal basal area, basal area longitudinally rugulose over entire horizontal portion; supraclypeal area longitudinally striolate, impunctate; mesopleura dull between close punctures ..... *basalis* (F. Smith)

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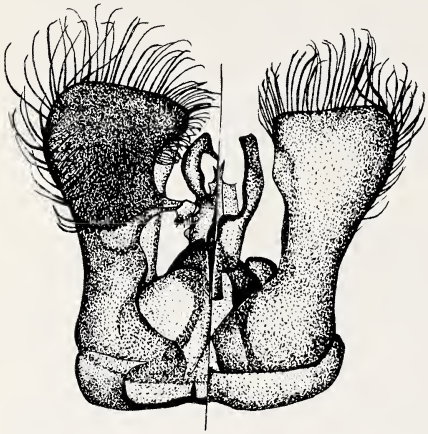
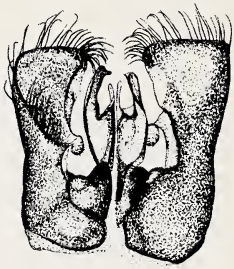




*basalis* *nunenmacheri*

Figure 1. Genitalia of *Cephalylaeus* males; right half indicates dorsal aspect, left half indicates ventral aspect. Figures by Ruth Ann DeNicola.

### **Hylaeus (Cephalylaeus) basalis** (F. Smith)

*Prosopis basalis,* F. Smith, 1853. Catalogue of Hymenoptera in the British Museum, 1:22. ♀ ♂.

*Prosopis basalis,* Metz, 1911. Trans. Amer. Ent. Soc., 37:102-103. ♀ ♂.

*Hylaeus (Cephalylaeus) basalis*, Michener, 1942. Jour. N.Y. Ent. Soc., 50:274. Mitchell, 1960. Tech. Bul. 141, North Carolina Agr. Exp. Sta., pp. 76-77.

This is a widely distributed species in montane areas of the United States and Canada. In the southern portions of its range it is found only at high elevations in the various major north-south mountain ranges. It is, however, rarely taken in large numbers, and, like its close relative *H. nunenmacheri* Bridwell, exhibits a decided preference for flowers of the family Rosaceae.

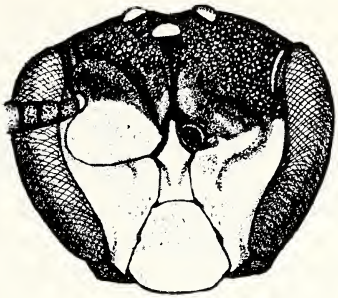
### **Hylaeus (Cephalylaeus) nunenmacheri** Bridwell

*Hylaeus nunenmacheri* Bridwell, 1919. Proc. Haw. Ent. Soc., 4:157. ♀.

*Hylaeus (Cephalylaeus) nunenmacheri*, Michener, 1942, Jour. N.Y. Ent. Soc., 50:274.

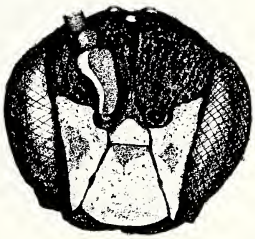
This species superficially resembles the preceding species but is smaller and less robust; it may be separated from *H. basalis* by the key given above. Although presently known only from California, where it occurs from sea

*aztecus*



*basalis*

*nunenmacheri*



*sparsus*

Figure 2. *Hylaeus* species. Aspects of the male faces. Figures by Ruth Ann DeNicola.

level to moderate elevations in the Coast Ranges and Sierra Nevada, *H. nunenmacheri* undoubtedly will be found in Oregon, Nevada, and Baja California.

KEY TO SPECIES OF *METZIELLA*

1. Males ..... *sparsus* (Cresson)
   Females ..... 2
2. Propodeum with distinct more or less horizontal basal area which is almost twice as long as median length of postscutellum ..... *hydrangeae* Mitchell

   Propodeum usually evenly sloping from base to apex; if a horizontal basal area present, it does not exceed median length of postscutellum ..... *sparsus* (Cresson)

### **Hylaeus (Metziella) sparsus sparsus** (Cresson)

*Prosopis sparsa* Cresson, 1869. Proc. Boston Soc. Nat. Hist., 12:271. ♀.
*Prosopis thaspii* Robertson, 1898. Trans. Acad. Sci. St. Louis, 8:43. ♀.
*Prosopis potens* Metz, 1911. Trans. Amer. Ent. Soc., 37:103. ♂.
*Prosopis modestus,* Metz, 1911. *Op. cit.,* p. 121, (in part).
*Hylaeus* (*Metziella*) *potens,* Michener, 1942. Jour. N.Y. Ent. Soc., 50:2743; Mitchell, 1960. Tech. Bul. 141, North Carolina Agr. Exp. Sta., p. 78.

This species ranges from southeastern Canada to Georgia and westward to central Texas. Specimens which I have seen from Texas tend toward fuller maculae.

### **Hylaeus (Metziella) hydrangeae** Mitchell

*Hylaeus* (*Metziella*) *hydrangeae* Mitchell, 1951. Jour. Elisha Mitchell Sci. Soc., 67:244. ♀.

A single female, which agrees quite closely with Mitchell's original description of this species, is the second known specimen of this apparently rare species. It was collected at Ft. Gordon, Richmond Co., Georgia, June 14, 1959 (R. R. Snelling; LACM).

Since the male of *H. hydrangeae* remains unknown, it cannot be included in the key, but may be expected to exhibit the long basal area of the propodeum which is characteristic of the female; in all probability the pronotal collar will be maculate, a further character to separate it from typical *H. sparsus.*

### **Hylaeus (Hylaeana) aztecus** (Cresson)

*Prosopis azteca* Cresson, 1869. Proc. Boston Soc. Nat. Hist., 12:272. ♀.
*Hylaeus aztecus,* Cockerell, 1924. Proc. Calif. Acad. Sci., Ser. 4, 12:530.

This is a widely distributed Mexican species which has recently been collected in southern California, Arizona, and Texas. Examination of the male terminalia indicates that this species should be assigned to the subgenus *Hylaeana.*

New records: California: 1 ♀, In-Ko-Pah Gorge, 9 mi W Coyote Wells, Imperial Co., III-26-1961 (J. Powell; CIS), on *Hyptis emoryi.* Arizona: 1 ♀, Gardner Can. Rd., Santa Rita Mts., Pima Co., X-19-1957 (G. D. Butler; UA); 1 ♀, Ruby, Pima Co., VIII-16-1961 (F. G. Werner; UA); 1 ♂, Ft. Huachuca, 11 mi NW, VII-10-1952 (R. H. and L. D. Beamer, C. Liang and W. E. LaBerge; UK), on *Verbesina encelioides.* Texas: 1 ♂, Progreso, IV-12-1950 (R. H. and L. D. Beamer, W. P. Stephen, C. D. Michener, J. G. and B. L. Rozen); 1 ♀, Brownsville, IV-17-1952 (C. D. Michener, R. H. and L. D. Beamer, A. Wille, W. E. LaBerge); 1 ♂, Southmost, IV-13-1950 (R. H. and L. D. Beamer, W. P. Stephen, C. D. Michener, J. G. and B. L. Rozen; all UK). Baja California del Norte: 1 ♀, San Felipe, 3 mi SW, III-29-1963 (G. I. Stage; LACM).

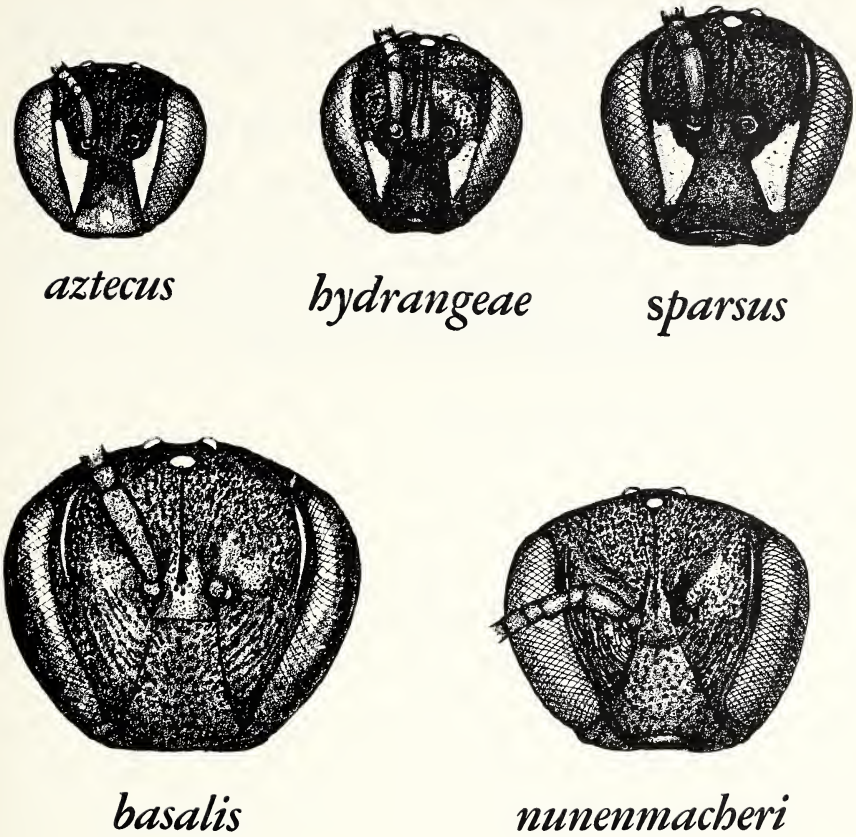



Figure 3. *Hylaeus* species. Aspects of the female faces. Figures by Ruth Ann DeNicola.

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Werner, University of Arizona (UA); Gerald I. Stage (GIS). Specimens from the collection of the author and of the Los Angeles County Museum of Natural History are indicated (LACM). The illustrations were prepared by Ruth Ann DeNicola.

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# THREE NEW EPITONIID GASTROPODS FROM THE PANAMIC PROVINCE

*By* HELEN DUSHANE AND JAMES H. MCLEAN

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DOROTHY M. HALMOS
*Editor*

# THREE NEW EPITONIID GASTROPODS FROM THE PANAMIC PROVINCE

*By* HELEN DUSHANE[1] AND JAMES H. MCLEAN[2]

ABSTRACT: Three new Epitoniids are described from Mexico: *Epitonium (Asperiscala) huffmani* from the upper reaches of the Gulf of California, *Epitonium (Epitonium) shyorum* from Manzanillo, and *Amaea (Scalina) tehuanarum* from the Gulf of Tehuantepec.

Three striking new species of Epitoniidae are described herein. One has been unidentified in the Los Angeles County Museum of Natural History (LACM), another was dredged by Laura and Carl Shy off Manzanillo, Mexico, the third was taken in the Gulf of Tehuantepec during a reconnaisance trip made by Captain Xavier Mendoza and Dr. Donald Shasky.

ACKNOWLEDGMENTS

We are indebted to the collectors mentioned above for making the specimens available to us. Dr. Myra Keen has kindly read and criticized the manuscript. Photographs are by Mr. Mike Hatchimonji, museum photographer.

## **Epitonium (Asperiscala) huffmani,** new species

Fig. 1

*Diagnosis*: An *Epitonium* distinguished from other west American species in having few, rapidly expanding whorls, brown ground color, numerous low axial ribs, and fine spiral ribs.

*Description*: Shell small, brown, periostracum lacking; nuclear whorls two, smooth, brown, glassy; third whorl white, axially ribbed; the following five whorls brown, strongly convex, rapidly enlarging, thin and fragile, with fine, white axial costae and white raised spiral threads between the costae, forming small, precise rectangles when intercepted by the costae; the final whorl lighter in color and the base of the shell fading to white adjacent to the columella; shell lacking a basal ridge; outer lip thin and white; umbilicus lacking; operculum missing in holotype. Dimensions (in mm): length 11, width 7 (holotype).

*Type Locality*: Cholla Bay, Bahía Adair, Sonora, Mexico, latitude 31° 21′ N, longitude 113° 40′ W, collected April 1937 by Al Huffman.

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[2]Curator of Invertebrate Zoology, Los Angeles County Museum of Natural History.

*Type Material*: Holotype, LACM, Invertebrate Zoology Type Collection, cat. no. 1159.

*Referred Material*: An additional specimen having a fractured outer lip has been examined. It was collected by Mrs. Faye B. Howard in February 1967 at the outer side of San Carlos Bay, near Guaymas, Sonora, Mexico, latitude 27° 56′ N, longitude 111° 05′ W, and is now in the collection of the Santa Barbara Museum of Natural History. Dimensions (in mm): length 9, width 5.

*Discussion*: This species differs from any other known from the Panamic province. It is similar in proportion to, but lacks the umbilicus of *Epitonium* (*Asperiscala*) *billeeana* (DuShane and Bratcher, 1965), recently removed from the genus *Scalina* by DuShane (1967). In detail of sculpture the two species are only superficially similar.

*Epitonium huffmani* is named for Al Huffman who collected extensive material from the Gulf of California during the 1930's and whose collection is now in the Los Angeles County Museum of Natural History.

## **Epitonium (Epitonium) shyorum,** new species

Fig. 2

*Diagnosis*: A small slender species differing from others in having tabulate, spinose whorls, angulate base, incomplete peritreme and 9 costae per whorl.

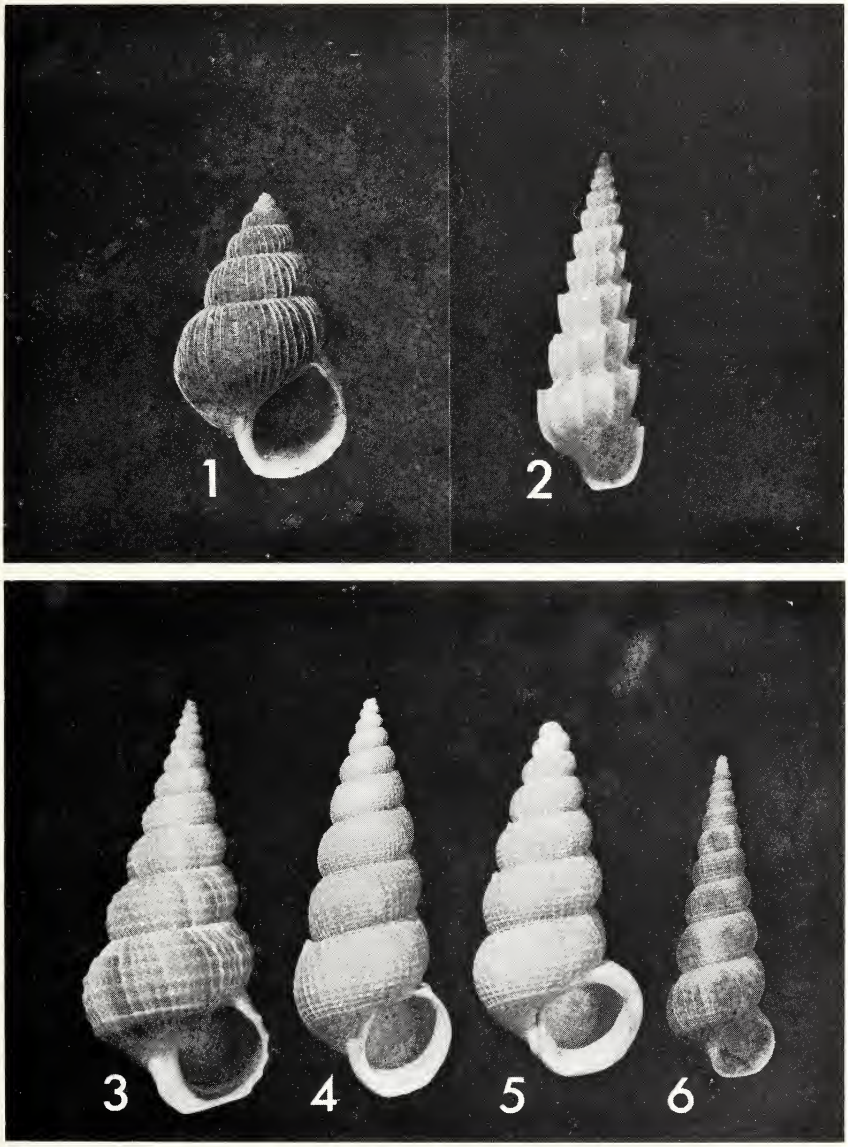
*Description*: Shell small, white, tall, with 8 to 9 flaring costae, continuous from whorl to whorl, with an angular spine at the shoulder of each whorl; the ribs least pronounced on the lower portion of the body whorl; nuclear whorls 3, smooth, convex, brown, and glassy; postnuclear whorls 10; suture distinct but not deeply impressed; umbilicus lacking; surface area between costae lacking spiral sculpture; whorls flat sided, angulate at the shoulder and at the base; basal disk or cord lacking; aperture oval, but lip reflecting angulate outline of the costae, with a right angled spine on the shoulder; inner lip lacking; operculum missing in type. Dimensions (in mm): length 12; width 4 (holotype).

*Type Locality*: Manzanillo, Colima, Mexico, latitude 19° 03′ N, longitude 104° 20′ W. Dredged in 12 to 13 fms (21 to 25 m), broken shell and sand bottom, by Laura and Carl Shy, November 1965; 6 specimens.

*Type Material*: Holotype, LACM, Invertebrate Zoology Type Collection, cat. no. 1160; 1 paratype, Stanford University; 1 paratype, California Academy of Sciences; 2 paratypes, Shy collection; 1 paratype, DuShane collection.

*Referred Material*: One specimen in the LACM collection was dredged by the *Velero III* at Station 682-37, 15 March 1937, off Concepcion Bay, Baja California, Mexico, at latitude 26° 53′ N, longitude 111° 52′ W in 12 fms (21 m). The specimen has 9 costae and 10 whorls; all but one of the nuclear whorls are missing. Dimensions (in mm): length 10; width 3.

*Discussion*: *Epitonium shyorum* does not suggest comparison with other




Figures 1-6. 1. *Epitonium* (*Asperiscala*) *huffmani*, new species. Holotype, LACM 1159. X 4. 2. *Epitonium* (*Epitonium*) *shyorum*, new species. Holotype, LACM 1160. X 4. 3. *Amaea* (*Scalina*) *ferminiana* (Dall). Gulf of Tehuantepec, Mexico. DuShane coll. X 1.5. 4. *Amaea* (*Scalina*) *tehuanarum*, new species. Holotype, LACM 1161. X 1.5. 5. *A. tehuanarum*. Paratype, DuShane coll. X. 1.5. 6. *Amaea* (*Scalina*) *brunneopicta* (Dall). Gulf of Tehuantepec, Mexico. DuShane coll. X. 1.5.

Panamic species. The characteristic stepped outline of the shell and the absence of the inner lip readily distinguish it.

The name honors Laura and Carl Shy of Westminister, California, who are contributing much to our knowledge through their finds of rare Panamic mollusks.

**Amaea (Scalina) tehuanarum,** new species

Figs. 4, 5

*Diagnosis*: An *Amaea* distinguished from the 2 other Panamic species in having intermediate proportions, a thickened mature lip, and a convex outline to the overall slope of the shell.

*Description*: Shell large, thin but strong, light brown, with 9 to 10 gradually enlarging postnuclear whorls (nuclear whorls missing); the first three or four whorls showing a decided angulation at the periphery, the following whorls markedly convex; sculpture strongly cancellate throughout, with 9 spiral ribs on the fourth whorl, increasing to 15 on the penultimate whorl; ribs more closely spaced and narrow below the deeply impressed suture, fine spiral striae between the spiral ribs; axial sculpture of 38-40 thin, white costae, raised into aculeated lamellae at the suture and reflected toward the direction of growth; fine axial striae between the axial costae; base of shell set off by a ridge consisting of a spiral cord of regular strength; base of shell with about 14 thin, closely spaced spiral cords, crossed by the much reduced axial ribs; umbilicus lacking; aperture simple, white; lip greatly thickened by one or more coalesced axial ribs; columella heavier and slightly deflected at its lower portion, with, on some specimens, a slight twisting behind the columellar lip; peritreme discontinuous and attached on the inner face of the last whorl, with cancellate sculpture of the base often seen showing through the glazed surface within the peritreme; operculum missing in type lot. Dimensions (in mm): length 39.5; width 15 (holotype).

*Type Locality*: Gulf of Tehuantepec, Mexico; dredged in 59-68 meters, mud bottom, latitude 15° 58′ N, longitude 95° 00′ W, Donald Shasky and Xavier Mendoza, July 1963; 13 specimens, none live-collected.

*Type Material*: Holotype, LACM, Invertebrate Zoology Type Collection, cat. no. 1161, paratype, cat. no. 1162. Additional paratypes will be distributed to Stanford University, California Academy of Sciences, Santa Barbara Museum of Natural History, United States National Museum, and to the Shasky and DuShane private collections.

*Referred Material*: One specimen in the LACM collection was trawled in 30 fathoms off Punta San Telmo, in the southwestern part of the Gulf of California, latitude 25° 18′ N, longitude 110° 57′ W, by Lloyd Findley, 10 July 1965. The specimen was live-collected, has 10 postnuclear whorls, and has a paucispiral operculum of three whorls. It measures (in mm) length 44, width 17. Another specimen in the Museum collection was dredged by the *Velero III*

at Station 539-36, March 1936, off the spit at Bahía de Los Angeles, Baja California, at latitude 28° 53′ 40″ N, longitude 113° 32′ 45″ W, in one fathom, sand bottom. The specimen has 8 postnuclear whorls and measures (in mm) length 39, width 15.5. These two specimens are darker than those of the type series, none of which were collected alive, indicating that the color has probably faded in the type series.

*Discussion*: *Amaea tehuanarum* is closely related to *Amaea brunneopicta* (Dall, 1908: 316, pl. 8, fig. 10), *Amaea ferminiana* (Dall, 1908: 318, pl. 8, fig. 8), but differs from both of these species in proportions. The shell is broader than *A. brunneopicta* and narrower than *A. ferminiana*. Both *A. ferminiana* and *A. brunneopicta* have evenly tapering shells while that of *A. tehuanarum* is rapidly inflated, giving a convex outline to the overall slope of the shell. In addition, the thickened lip of *A. tehuanarum* is lacking in specimens examined of either of the two species of Dall, each of which has a thin fragile lip. *Amaea ferminiana* reaches twice the length of *A. tehuanarum*.

Although Keen (1958: 278), treated the two species of Dall as differing only subspecifically, they differ consistently in proportion and have generally been accepted as valid species. Specimens have been seen from many localities at which both species occur. Both *A. ferminiana* and *A. brunneopicta* occur in the Gulf of Tehuantepec along with *A. tehuanarum*. Specimens of *A. ferminiana* (fig. 3) and *A. brunneopicta* (fig. 6) from this locality are illustrated here for comparison.

Although Keen (1958: 278) treated *Scalina* as a full genus, we are following Clench and Turner (1950: 242) in regarding it as a subgenus of *Amaea*. The genus *Amaea* H. and A. Adams, 1853, type species *Scalaria magnifica* Sowerby (Kira, 1962: 30, pl. 14, fig. 20), shows, on the type species, a weak basal ridge without having the basal sculpture greatly different from that on the body whorl. In the subgenus *Scalina* Conrad, 1865, type species *Scalina staminea* Conrad (Palmer, 1937: 102, pl. 8, fig. 16), a stronger basal ridge is apparent, the basal area is markedly concave, and the basal sculpture is radically different from that on the body whorl. As shown by Palmer (1937) and Clench and Turner (1951: 287), *Ferminoscala* Dall, 1908, type species *Epitonium (Ferminoscala) ferminianum* Dall, is a synonym of *Scalina*. Clench and Turner (1950) placed the Caribbean species *Amaea retifera* Dall in the subgenus *Scalina* (inadvertently as *Ferminoscala*) since the basal ridge and concave base is quite apparent in that species, but we feel that the Caribbean species *Amaea mitchelli* Dall should also have been assigned by them to the subgenus *Scalina*, rather than to *Amaea s. str.* It is clearly a species analogue of *A. ferminiana* and differs chiefly in having less pronounced axial and spiral sculpture.

*Amaea tehuanarum* is named for a group of Zapotec Indians, the Tehuanos, who inhabit the region of the Isthmus of Tehuantepec. The Tehuanas are the women of the tribe who control the market places, have a dignity

of bearing and a great self sufficiency (Covarrubias 1947: 39, 246). They are famous for their caracol skirts made from handwoven material, dyed purple with the secretion from the rock shell *Purpura patula pansa* Gould.

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# OTOLITHS AND OTHER FISH REMAINS FROM THE TIMMS POINT SILT (EARLY PLEISTOCENE) AT SAN PEDRO, CALIFORNIA

*By* JOHN E. FITCH

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DOROTHY M. HALMOS
*Editor*

# OTOLITHS AND OTHER FISH REMAINS FROM THE TIMMS POINT SILT (EARLY PLEISTOCENE) AT SAN PEDRO, CALIFORNIA

*By* John E. Fitch[1]

Abstract: Over 1,000 pounds of fossiliferous Timms Point silt yielded 2,601 otoliths, 121 vertebrae, 68 teeth, 2 dermal denticles, and 1 fin spine. These remains had come from a minimum of 62 species (53 bony fishes and 9 elasmobranchs) belonging to 54 genera in 30 families. Nine of the 53 teleost species belong to two families of deep-sea fishes (Myctophidae and Melamphaidae) that seldom have been captured in water shallower than 1,000 feet, and six other species are "northern" forms that have not been noted within several hundred miles of the Timms Point locality during modern times.

An exposure of Timms Point silt near the type section at San Pedro, California, was sampled by personnel from the Los Angeles County Museum of Natural History on several occasions during the past decade. Fossiliferous matrix collected at this site (LACMIP 130) during these field trips was washed and processed as explained in a previous publication (Fitch, 1966), and all fish remains were removed and saved. A small number of fish remains recovered by Museum personnel working under the supervision of George P. Kanakoff, then Curator of Invertebrate Paleontology, was also used in this study, as were many otoliths found by Dr. Charles R. Wright, Sanger, California, in material he had collected at Timms Point during recent years. In addition, 94 otoliths, 3 teeth, and 1 dermal denticle identified for William Zinsmeister, Long Beach, California, during January and February 1968, have been retained in his collection. These remains represented at least 20 species (2 elasmobranchs and 18 teleosts), two of which, *Prionace glauca* and *Squatina californica,* were not among the 2,507 otoliths, 65 teeth, and 1 dermal denticle previously examined from this deposit.

Clark (1931) described three units of Timms Point silt, and at the type locality (Timms Point), the exposed thickness of these three units is "30 to 80 feet, but the maximum computed thickness is about 120 feet" according to Woodring, Bramlette, and Kew (1946).

Geologists and paleontologists agree that the Timms Point silt was deposited after the Lomita marl and before the San Pedro sand. Although it generally has been accepted that the Lomita marl is early Pleistocene in age, my otolith investigations and recent work of others on molluscan assemblages (Kanakoff and McLean, 1966; Kanakoff, pers. commun.; and S. S. Berry, pers. commun.) suggest the Lomita marl is probably the youngest marine Pliocene

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TABLE 1

Fish Remains Found in the San Pedro, California, Timms Point Pleistocene

| *Scientific name* | *Common name* | *Type and number of remains* | | | |
|---|---|---|---|---|---|
| | | *otoliths* | *teeth* | *vertebrae* | *other* |
| | ELASMOBRANCHS | | | | |
| *Carcharodon carcharias* | white shark | | 2 | | |
| *Galeorhinus zyopterus* | soupfin shark | | 9 | | |
| *Heterodontus francisci* | horn shark | | 1 | | |
| *Isurus oxyrinchus* | mako | | 7 | | |
| *Prionace glauca*[1] | blue shark | | 1 | | |
| *Raja* spp. | skates | | 16 | | 1* |
| *Squalus acanthias* | spiny dogfish | | 19 | | |
| *Squatina californica*[1] | Pacific angel shark | | | | 1† |
| *Triakis semifasciata* | leopard shark | | 1 | | |
| | TELEOSTS | | | | |
| *Ammodytes hexapterus* | sandlance | 8 | | | |
| *Artedius notospilotus* | bonehead sculpin | 6 | | | |
| *Atheresthes stomias* | arrowtooth flounder | 1 | | | |
| *Atherinops affinis* | topsmelt | 2 | | | |
| *Brosmophycis marginata* | red brotula | 15 | | | |
| *Ceratoscopelus townsendi* | dogtooth lightfish | 1 | | | |
| *Chitonotus pugetensis* | roughback sculpin | 7 | | | |
| *Citharichthys sordidus* | Pacific sanddab | 16 | | | |
| *Citharichthys stigmaeus* | speckled sanddab | 25 | | | |
| *Citharichthys xanthostigma* | longfin sanddab | 22 | | | |
| *Citharichthys* spp. | sanddabs | 267 | | | |
| *Clupea pallasi* | Pacific herring | 5 | | | |
| *Coryphopterus nicholsi* | bluespot goby | 276 | | | |
| cottids | sculpins | 419 | | | |
| *Cymatogaster aggregata* | shiner perch | 114 | | | |
| *Diaphus theta* | California headlightfish | 10 | | | |
| *Electrona rissoi* | chubby flashlightfish | 8 | | | |
| embiotocids[1] | surfperches | 7 | | | |
| *Engraulis mordax* | northern anchovy | 4 | | | |
| *Enophrys taurina* | bull sculpin | 6 | | | |
| *Genyonemus lineatus* | white croaker | 8 | | | |
| *Glyptocephalus zachirus* | rex sole | 45 | | | |
| *Icelinus burchami* | dusky sculpin | 1 | | | |
| *Icelinus filamentosus* | threadfin sculpin | 7 | | | |
| *Icelinus fimbriatus* | fringed sculpin | 7 | | | |
| *Icelinus quadriseriatus* | yellowchin sculpin | 43 | | | |
| *Icelinus tenuis* | spotfin sculpin | 11 | | | |
| *Lampadena urophaos* | sunbeam lampfish | 1 | | | |
| *Leptocottus armatus* | Pacific staghorn sculpin | 3 | | | |
| *Lethops connectens* | halfblind goby | 78 | | | |
| *Lycodopsis pacifica* | blackbelly eelpout | 34 | | | |
| *Lyconectes aleutensis* | dwarf wrymouth | 25 | | | |

TABLE 1 *(continued)*

Fish Remains Found in the San Pedro, California, Timms Point Pleistocene

| *Scientific name* | *Common name* | *Type and number of remains* | | | |
|---|---|---|---|---|---|
| | | *otoliths* | *teeth* | *vertebrae* | *other* |
| *Lyopsetta exilis* | slender sole | 219 | | | |
| *Malacocottus zonurus* | blackfin sculpin | 4 | | | |
| *Melamphaes lugubris* | black bigscale | 1 | | | |
| *Merluccius productus* | Pacific hake | 22 | | | |
| *Microgadus proximus* | Pacific tomcod | 11 | | | |
| *Microstomus pacificus* | Dover sole | 1 | | | |
| *Otophidium taylori* | spotted cusk-eel | 113 | | | |
| *Oxyjulis californica* | señorita | 2 | | | |
| *Parophrys vetulus* | English sole | 24 | | | |
| *Pimelometopon pulchrum* | California sheephead | | 4 | | |
| *Porichthys notatus* | plainfin midshipman | 101 | | | |
| *Protomyctophum crockeri* | California flashlightfish | 8 | | | |
| *Radulinus asprellus* | slim sculpin | 81 | | | |
| *Scopelogadus bispinosus* | twospine bigscale | 1 | | | |
| *Sebastodes goodei* | chilipepper | 1 | | | |
| *Sebastodes hopkinsi* | squarespot rockfish | 1 | | | |
| *Sebastodes rosaceus* | rosy rockfish | 1 | | | |
| *Sebastodes* spp. | rockfish | 464 | | | |
| *Sebastolobus* sp. | channel rockfish | 3 | | | |
| *Seriphus politus* | queenfish | 8 | | | |
| *Stenobrachius leucopsarus* | northern lampfish | 35 | | | |
| *Tarletonbeania crenularis* | blue lanternfish | 10 | | | |
| *Theragra chalcogramma* | walleye-pollack | 4 | | | |
| *Trachurus symmetricus* | Pacific jackmackerel | 1 | | | |
| *Xeneretmus* cf. *latifrons* | blackedge poacher | 2 | | | |
| | unidentified teleosts | 2 | 8 | 121 | 1** |

*skate "wing" spine
**fin ray spine
†dermal denticle
[1]in William Zinsmeister collection

in the Los Angeles area. This being the case, the Timms Point silt would be the oldest Pleistocene of the region.

No age estimate is available for the Timms Point silt, but a potassium-argon analysis of glauconite from the Lomita marl has yielded an estimate of 3.04 million years before the present (B.P.) for that unit (Obradovich, 1965). Fanale and Schaeffer (1965), utilizing helium-uranium and ionium radiometric ratios and measurements, estimated the age of the 1200-foot terrace of the Palos Verdes hills as $>300{,}000$ years (5 samples) and $325{,}000 \pm 60{,}000$ years (1 sample). This marine terrace is the oldest late Pleistocene of southern California, having been laid down after the San Pedro sand. Unfortunately, because Fanale and Schaeffer (1965) report that the Lomita marl is

intermediate in age between the 70- and 1,200-foot terraces, considerable doubt is cast upon the validity of their techniques for determining geochronology.

Valentine (1961), using data for molluscan assemblages, speculated that the Timms Point silt was deposited at depths between "about 25 and 100 fathoms, and waters at those depths were cooler in some season [*sic*] at least than at present." The fish remains that I identified (Table 1) lend support to these theories of depth and temperature. In all, 2,601 otoliths, 121 vertebrae, 68 teeth (56 from elasmobranchs and 12 from teleosts), 2 elasmobranch dermal denticles, and 1 fin spine were recovered from 1,000 pounds or more of fossiliferous matrix excavated from this site. These items represent a minimum of 53 species of bony fishes (teleosts) and 9 of sharks, skates, and rays.

Previously, only Bagg (1912) had noted teleost remains from the Timms Point silt, but his report, comprising a single plate (Pl. 28 a-e) illustrating five assorted sagittae, fails to identify them except as otoliths. Unfortunately, two of these (figures c and e) show outer faces, so they are identifiable only as cottids (Cottidae); however, his figures a, b, and d are of *Tarletonbeania crenularis, Sebastodes* sp., and *Cymatogaster aggregata,* respectively. Clark (1931) listed shark teeth (3 or fewer specimens at 1 of 15 stations) in one of his tables. He questionably identified these as "*Galeus zyopterus.*" Nine of the 56 elasmobranch teeth that I identified (Table 1) were from this species (*Galeorhinus zyopterus*).

Most of the Timms Point silt exposures mentioned by Arnold (1903), Clark (1931), and Woodring *et al.* (1946) have long since disappeared, and at the present rate of human encroachment, another decade could see the last surface outcrop of this important horizon covered by a building, highway, retaining wall, or some similar "mark of progress." Thus, unless some concerted effort is made to salvage additional fossiliferous Timms Point silt in the near future, the small handful of otoliths, teeth and other remains reported here may be our only record of the fish fauna during the million years or so of geologic history required to deposit this material. Except for a small amount of material in the Zinsmeister collection, the otoliths and other fish remains reported upon here are deposited in the Los Angeles County Museum of Natural History; the figured specimens have been curated separately.

## SYSTEMATIC ACCOUNT

### Heterodontidae—horn sharks

*Heterodontus francisci* (Girard)—horn shark

Horn sharks are abundant in rocky subtidal areas between about Morro Bay, California, and Magdalena Bay, Baja California. They seldom move about during daylight hours, but at night they can be found foraging the bottom for food, primarily crustaceans. During their nocturnal feeding, they occasionally stray into areas of sandy or sandy-mud bottoms. They are reported to

attain a length of about 4 feet, but the largest I have seen was 3 feet 2⅛ inches long and weighed 22 pounds. Horn shark teeth have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1966, and unpublished data; Kanakoff, 1956).
*Material*: 1 tooth.

Isuridae—mako sharks

*Carcharodon carcharias* (Linnaeus)—white shark

The white shark, an inhabitant of temperate and subtropical waters throughout the world, ranges from Alaska to Mazatlan, Mexico, in the eastern north Pacific (Kato, 1965). A large individual for our coast would be 12 to 15 feet long, although white sharks are reported (unreliably) to attain 35 feet. This species probably is responsible for most of California's unprovoked attacks on swimmers and bathers, usually occurring in relatively shallow water near shore. White shark teeth have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1964, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956).
*Material*: 2 teeth.

*Isurus oxyrinchus* Rafinesque—mako

This world-ranging species is fairly common in our coastal waters between about San Francisco and Magdalena Bay, Baja California. An 11-footer from Santa Catalina Island, California, is the largest authentic record for the species, but the usual mako in the eastern north Pacific is shorter than 8 feet. Mako remains, primarily teeth, have been found in numerous southern California Pliocene and Pleistocene deposits, sometimes reported as *I. glaucus* (Fitch, 1964, 1967, and unpublished data; Kanakoff, 1956).
*Material*: 7 teeth.

Triakidae—smoothhounds

*Triakis semifasciata* Girard—leopard shark

Leopard sharks have been caught at many localities between Oregon and Mazatlan, Mexico. They usually frequent shallow areas where the bottom is sandy, but they also abound in rocky areas, especially around southern California's coastal islands. Females grow larger than males and may reach lengths of 7 feet, but a 5-foot, 35-pounder can be considered quite large. Leopard shark remains have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967 and unpublished data; Fitch and Reimer, 1967).
*Material*: 1 tooth.

Carcharhinidae—requiem sharks

*Galeorhinus zyopterus* Jordan and Gilbert—soupfin shark

The soupfin shark ranges from northern British Columbia to about

Magdalena Bay, but is not abundant at the more southerly latitudes. Females occur principally south of Point Conception, usually at depths of 100 to 600 feet or more. A 6½-foot female may weigh as much as 100 pounds, but 50- to 70-pounders are most often encountered. Soupfin shark remains, mostly teeth, have been reported from the Timms Point silt (Clark, 1931), and have been found in numerous other southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956).
*Material*: 9 teeth.

*Prionace glauca* (Linnaeus)—blue shark

The blue shark is a pelagic species occurring in tropical, subtropical, and warm temperate areas of all world seas. Along the southern California coast they are extremely abundant during summer months, and they almost invariably are males. Twelve-footers have been caught off California (close to record size for the species), but our usual blue shark will not exceed 6 feet and 50 pounds. Blue shark remains are not abundant in fossil deposits, being known from only a few other localities (Fitch, unpublished data).
*Material*: 1 tooth in the Zinsmeister collection.

Squalidae—dogfish sharks

*Squalus acanthias* Linnaeus—spiny dogfish

The spiny dogfish abounds in the north Pacific Ocean (eastern and western), ranging south on our coast to Sebastian Viscaino Bay, Baja California. Females attain larger sizes than males, and are reported to reach 5 feet, but a 4-footer is rare. Trawling off southern California yields the best spiny dogfish catches in 100 to 250 feet of water, but they have been caught as deep as 1,200 feet. Remains of *Squalus acanthias* have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967 and unpublished data).
*Material*: 19 teeth.

Squatinidae—angel sharks

*Squatina californica* Ayres—Pacific angel shark

Although the Pacific angel shark ranges from southern Alaska into the Gulf of California, it is not abundant north of Point Conception nor south of Magdalena Bay. They seem to prefer sandy or sandy mud bottoms at depths of 50 to 70 feet, but many are taken or seen in 6 to 8 feet of water and others in 150 feet or deeper. A 44-inch female, the largest I have seen, weighed 31 pounds. *Squatina* remains have been found in many Pliocene and Pleistocene deposits in southern California (Fitch, 1964, 1967, and unpublished data).
*Material*: 1 dermal denticle in the Zinsmeister collection.

### Rajidae—skates

*Raja* spp.—skates, species undetermined

There do not appear to be any foolproof tooth characters for distinguishing the six species of skates that occur off California. At various times, one or more of these six skates can be captured at any depth from the shallow subtidal to several thousand feet. Four of the species (*R. inornata, R. stellulata, R. trachura,* and *R. kincaidi*) are "small" forms which probably never exceed lengths of 2½ feet (including tail) as adults. *R. rhina* is reported to attain 4 to 5 feet, and *R. binoculata* may reach 8 feet and exceed 150 pounds. Skate remains, mostly teeth and "wing" spines, have been found in numerous southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data).

*Material*: 16 teeth and 1 wing spine.

### Clupeidae—herrings

*Clupea pallasi* Valenciennes—Pacific herring

The Pacific herring, a schooling fish, ranges throughout the north Pacific Ocean (eastern and western), but because of pollution and bay development, herring seldom are observed south of Point Conception at present, although they were abundant in San Diego Bay three decades ago. Pacific herring are said to attain lengths of 18 inches, but a 12- to 14-inch individual is considered quite large. Pacific herring otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967 and unpublished data). The sagittae of a large, adult Pacific herring will exceed 5.0 mm in length.

*Material*: 5 otoliths from 2.9 to longer than 3.3 mm (Fig. 1a).

### Engraulidae—anchovies

*Engraulis mordax* Girard—northern anchovy

The northern anchovy, a schooling fish, ranges from British Columbia to Magdalena Bay, and offshore for more than 100 miles. It is reported to attain a length of 9 inches, but the largest I have seen was an 8-inch fish that weighed 2 ounces. Otoliths of *E. mordax* have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967). The sagittae of a large, adult northern anchovy will exceed 4.5 mm in length.

*Material*: 4 otoliths from 2.8 to 4.1 mm long (Fig. 1b).

### Myctophidae—lanternfishes

*Ceratoscopelus townsendi* (Eigenmann and Eigenmann)—dogtooth lampfish

This little fish (attaining perhaps 4 inches when fully grown) is widely

distributed in tropical and temperate waters of the Pacific, Indian, and Atlantic Oceans. Along our coast, *C. townsendi* ranges from north of San Francisco to Magdalena Bay, Baja California, at least. Except at night, they seldom approach within 600 feet of the surface. Their otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult *C. townsendi* will exceed 3.0 mm in length.
*Material*: 1 otolith 2.6 mm long (Fig. 1c).

*Diaphus theta* Eigenmann and Eigenmann—California headlightfish

*Diaphus theta* ranges from the Gulf of Alaska to Cedros Island, Baja California, and offshore for several hundred miles, at least. They are reported to attain a length of 4½ inches (Clemens and Wilby, 1961), but in the central and southern parts of their range a 3½-inch individual is a rarity. At night, *D. theta,* along with other creatures that make up deep scattering layers, migrates upward and has been captured within 30 feet of the surface. During daylight hours it usually is found at depths of 1,000 feet or more. Otoliths of *D. theta* have been found in several southern California Pliocene and Pleistocene deposits, more than 400 having been recovered from a San Pedro, California (Lomita marl) deposit (Fitch, unpublished data). The sagittae of a large, adult *D. theta* will exceed 3.0 mm in length.
*Material*: 10 otoliths from 1.0 to 3.1 mm long (Fig. 1d).

*Electrona rissoi* (Cocco)—chubby flashlightfish

The chubby flashlightfish apparently lives in the scattering layers 1,000 feet or more beneath the surface during daylight hours but nearer the surface at night. It is rarely caught off California today, but may be abundant in other areas. In the eastern Pacific, it ranges from about Point Conception to Magdalena Bay, at least. The validity of the name *rissoi* is questionable for the form in the eastern north Pacific, but the otoliths found in this deposit match perfectly, in morphometry but not necessarily in size, the otoliths removed from a 1½-inch-long individual caught off our coast (the species attains 2¾ inches, at least). Otoliths of *E. rissoi* have been found in small numbers in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data; Fitch and Reimer, 1967). The sagittae of a large, adult *E. rissoi* will exceed 3.5 mm in length.
*Material*: 8 otoliths from 2.3 to 4.1 mm long (Fig. 1e).

*Lampadena urophaos* Paxton—sunbeam lampfish

*L. urophaos* ranges from about mid-Oregon to Magdalena Bay and offshore for a considerable distance. At night, it sometimes migrates to within about 150 feet of the surface, but during daylight hours it seldom is captured shallower than about 800 feet. This species may attain 5 inches when full grown. The otoliths of *L. urophaos* are larger than those of any other myctophid I have examined. (My comparative collection contains sagittae from more

than 100 myctophid species representing all but one of the recognized genera.) *L. urophaos* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult *L. urophaos* will exceed 7.5 mm in length.
*Material*: 1 incomplete otolith 4.0 mm long (Fig. 1i).

*Protomyctophum crockeri* (Bolin)—California flashlightfish

*P. crockeri* is distributed throughout the western and eastern north Pacific Ocean (apparently discontinuously), ranging on our coast from off Puget Sound to Cape San Lucas and offshore for a considerable distance. A large individual might measure 3 inches in total length, but few exceeding 2½ inches are caught. As with other myctophids, this species also approaches the surface at night, but not to the same extent, preferring to remain 500 feet deep or deeper. Otoliths of *P. crockeri* have been found in several southern California Pliocene and Pleistocene deposits, nearly 200 having been recovered from the Lomita marl (Pliocene) at San Pedro, California (Fitch, unpublished data). The sagittae of a large, adult *P. crockeri* will exceed 2.5 mm in length.
*Material*: 8 otoliths from 1.2 to 2.4 mm long (Fig. 1f).

*Stenobrachius leucopsarus* (Eigenmann and Eigenmann)—northern lampfish

*S. leucopsarus* is one of the most abundantly captured myctophids off California. It ranges from the Bering Sea to about Cedros Island and offshore for a considerable distance. At night it sometimes approaches to within 150 feet of the surface, returning to 750 feet or deeper during daylight hours. A large individual might measure 5 inches and weigh one-third of an ounce. Otoliths of *S. leucopsarus* have been found in many southern California Pliocene and Pleistocene deposits, more than 1,000 having been recovered from a San Pedro, California, (Lomita marl) deposit (Fitch, 1966, 1967, and unpublished data). The sagittae of a large, adult northern lampfish will exceed 1.8 mm in length.
*Material*: 35 otoliths from 0.8 to 2.0 mm long (Fig. 1g).

*Tarletonbeania crenularis* (Jordan and Gilbert)—blue lanternfish

The blue lanternfish ranges on our coast from northern Alaska to San Diego and offshore for a considerable distance. This species often migrates to the surface of the ocean at night, but during daylight hours it apparently prefers depths of 600 feet or more. It is reported to attain a length of 5½ inches, but off California a 4½-inch fish is unusual. Otoliths of *T. crenularis* have been found in several southern California Pliocene and Pleistocene deposits, more than 300 having been recovered from the Lomita marl (Pliocene) at San Pedro (Fitch, unpublished data). Bagg (1912) illustrated a sagitta of *T. crenularis,* but did not identify it beyond calling it an otolith. The sagittae of a large, adult blue lanternfish will exceed 1.8 mm in length.
*Material*: 10 otoliths from 1.2 to 2.0 mm long (Fig. 1h).

Merlucciidae—hakes

*Merluccius productus* (Ayres)—Pacific hake

Pacific hake range from Alaska to the southern tip of Baja California, and offshore for 350 miles or more. Sometimes they are found in shallow water near shore, but mostly they travel in dense schools near the bottom where the water is deeper than 600 feet. They are said to reach lengths of 3 feet, but a 30-inch fish is rare; a 26-inch female weighed slightly more than 4 pounds. *M. productus* otoliths have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, and unpublished data; Fitch and Reimer, 1967). The sagittae of a large, adult Pacific hake will exceed 30.0 mm in length.
*Material*: 22 otoliths from about 7.5 to longer than 26.0 mm (Fig. 1j).

Gadidae—cods

*Theragra chalcogramma* (Pallas)—walleye-pollack

The walleye-pollack inhabits bottom waters of the north Pacific (western and eastern), ranging south to about Monterey Bay on our coast. It is reported to reach a length of 3 feet and a weight of 7 or 8 pounds, but maximum sizes need authentication. Sagittae of *T. chalcogramma* have not been recovered from any fossil deposit except the Timms Point Pleistocene (this report), and a late Pleistocene deposit at San Pedro. The sagittae of a large, adult walleye-pollack will exceed 20.0 mm in length.
*Material*: 4 otoliths from 9.8 to 18.2 mm long (Fig. 1k).

*Microgadus proximus* (Girard)—Pacific tomcod

The Pacific tomcod ranges from Alaska to about Morro Bay, California, usually at depths of 200 feet or more, but sometimes in shallow water just outside the surf zone. A large individual might be 12 inches long but no weights are available for such a fish; a 10¼-inch female weighed just under 6 ounces. *M. proximus* otoliths are abundant in some southern California Pliocene deposits, and in the Pleistocene of northern California and Oregon (Fitch, unpublished data). The sagittae of a large, adult Pacific tomcod will exceed 14.0 mm in length.
*Material*: 11 otoliths 3.4 to larger than 6.0 mm (not figured).

Melamphaidae—bigscales

*Melamphaes lugubris* Gilbert—black bigscale

*M. lugubris* ranges from the Bering Sea to Cedros Island, Baja California, and offshore for a considerable distance. Although young individuals usually inhabit shallower depths and more-northerly waters than adults, black bigscales are most often captured 150 to 1,500 feet beneath the surface in quite deep water. They are reported to attain lengths of about 4½ inches. Otoliths of

*M. lugubris* have been found in only one other California deposit (Lomita marl Pliocene, San Pedro), but even there they are extremely rare (Fitch, unpublished data). The sagittae of a large, adult black bigscale will exceed 5.0 mm in length.
*Material*: 1 otolith 1.3 mm long (Fig. 1 l).

*Scopelogadus bispinosus* (Gilbert)—twospine bigscale

*S. bispinosus* ranges from about latitude 40° N. to latitude 20° S., and offshore across the Pacific. Young and half-grown individuals have been captured 400 feet beneath the surface and deeper, but adults seldom are captured within about 1,300 feet of the surface. The females attain larger sizes than males, reaching perhaps 4½ inches. Otoliths of *S. bispinosus* have been found in only one other California deposit (Lomita marl Pliocene, San Pedro), but even there they are very rare (Fitch, unpublished data). The sagittae of a large, adult twospine bigscale will exceed 2.0 mm in length.
*Material*: 1 otolith 2.0 mm long (Fig. 1m).

Bothidae—lefteyed flounders

*Citharichthys sordidus* (Girard)—Pacific sanddab

Pacific sanddabs are reported to range from southern Alaska to about Magdalena Bay, but their occurrence in central and southern Baja California needs to be verified. The maximum length and weight attributed to *C. sordidus* (16 inches and 2 pounds) also needs verifying. *Citharichthys* otoliths are abundant in most southern California Pliocene and Pleistocene deposits, and many of these are identifiable as *C. sordidus* (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967). The sagittae of a large, adult Pacific sanddab will exceed 8.0 mm in length.
*Material*: 16 otoliths from 4.2 to 6.7 mm long (Fig. 1n).

*Citharichthys stigmaeus* Jordan and Gilbert—speckled sanddab

Speckled sanddabs range along the coast from southeastern Alaska to Sebastian Viscaino Bay, Baja California, usually at depths shallower than 200 feet. A possible record-sized male just over 5½ inches long weighed just over 1 ounce. *C. stigmaeus* otoliths are abundant in most southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967). The sagittae from a large, adult speckled sanddab will exceed 3.5 mm in length.
*Material*: 25 otoliths from 1.7 to 2.9 mm long (Fig. 1o).

*Citharichthys xanthostigma* Gilbert—longfin sanddab

The longfin sanddab ranges from Monterey Bay, California, to about Magdalena Bay, usually in water shallower than 500 feet. It probably attains a maximum size somewhat in excess of 10 inches and 8 ounces. *C. xanthostigma*

otoliths are fairly abundant in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult longfin sanddab will exceed 7.0 mm in length.
*Material*: 22 otoliths from 3.0 to 7.3 mm long (Fig. 1p).

*Citharichthys* spp.—sanddabs, species undetermined

The otoliths of all three species of *Citharichthys* known to California are easily distinguished if they are in good condition, but most fossil sanddab otoliths are either worn or fragmented, making specific identification difficult if not impossible. Probably all three species are represented among the unidentified sanddab otoliths found in this deposit.
*Material*: 267 otoliths.

Pleuronectidae—righteyed flounders

*Atheresthes stomias* (Jordan and Gilbert)—arrowtooth flounder

The arrowtooth flounder ranges from the Bering Sea to Morro Bay, California, sometimes as shallow as 60 feet and other times as deep as 2,400. They are known to attain a length of 32¼ inches and a weight of 10 pounds—a 26-inch female weighed 6¼ pounds. *A. stomias* otoliths have been found in only one other fossil deposit (Lomita marl Pliocene, San Pedro), but even in that deposit they are rare (Fitch, unpublished data). The sagittae of a large, adult arrowtooth flounder will exceed 13.0 mm in length.
*Material*: 1 otolith 9.0 mm long (Fig. 1q).

*Glyptocephalus zachirus* Lockington—rex sole

The rex sole ranges from the Bering Sea to Ensenada, Baja California (at least), in from 25 to over 2,000 feet of water. They are reported to attain a maximum size of 22 inches and about 3 pounds. Rex sole otoliths are abundant in many southern California Pliocene and Pleistocene deposits (Fitch, 1967), more than 700 having been recovered from the Lomita marl Pliocene at San Pedro (Fitch, unpublished data). The sagittae of a large, adult rex sole will exceed 7.0 mm in length.
*Material*: 45 otoliths from 1.2 to 5.3 mm long (Fig. 1r).

*Lyopsetta exilis* (Jordan and Gilbert)—slender sole

The slender sole ranges from southeastern Alaska to Cedros Island, usually in depths of 400 to 800 feet, but sometimes as shallow as 120 feet or as deep as 1,700. A large individual might exceed 12 inches in length, but would not weigh more than ¼ pound. *L. exilis* otoliths have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967), more than 2,000 having been recovered from the Lomita marl Pliocene at San Pedro (Fitch, unpublished data). The sagittae of a large, adult slender sole will exceed 5.5 mm in length.
*Material*: 219 otoliths from 1.0 to 5.0 mm long (Fig. 1s).

*Microstomus pacificus* (Lockington)—Dover sole

The Dover sole ranges from northwestern Alaska to Ensenada (at least), usually at depths of 400 to 1,200 feet, but sometimes as shallow as 100 feet or as deep as 2,400. They are said to attain a maximum size of 30 inches and 10 pounds, but individuals exceeding 5 pounds are rarely seen. I have not found otoliths of *M. pacificus* in any other fossil deposit. The sagittae of a large, adult Dover sole will exceed 8.0 mm in length.
*Material*: 1 otolith 2.8 mm long (Fig. 1u).

*Parophrys vetulus* Girard—English sole

The English sole ranges from northwestern Alaska to Cedros Island, migrating inshore to spawn but living in deep water (to 1,000 feet) most of the remaining time. They attain a maximum size of 21 inches and about 3 pounds, but individuals exceeding 2 pounds are rarely seen. The otoliths of *P. vetulus* are difficult to distinguish from those of two other California flatfishes, *Eopsetta jordani* and *Lepidopsetta bilineata,* unless they are in perfect or near-perfect condition. Most of the Timms Point otoliths that I identified as *Parophrys* were in relatively poor condition. The sagittae of a large, adult English sole will exceed 9.0 mm in length
*Material*: 24 otoliths from 1.6 to longer than 6.5 mm (Fig. 1t).

Atherinidae—silversides

*Atherinops affinis* (Ayres)—topsmelt

Topsmelt range from the Straits of Juan de Fuca to and into the Gulf of California. Various subspecies inhabit bays, kelp beds, and offshore island areas where they live at or near the surface. A 14½-inch female weighing slightly less than 12 ounces appears to be a record size. *A. affinis* otoliths have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data). The sagittae of a large, adult topsmelt will exceed 5.0 mm in length.
*Material*: 2 otoliths from 2.1 to 4.4 mm long (Fig. 1v).

Carangidae—jacks

*Trachurus symmetricus* (Ayres)—Pacific jackmackerel

The Pacific jackmackerel, a schooling fish, is perhaps one of the three or four most abundant species off our coast, ranging from British Columbia to Cape San Lucas and offshore for several hundred miles. Jackmackerel are known to attain a length of 30 inches and a weight of 5 pounds, but most individuals in the commercial catch are smaller than 15 inches and 1 pound. *T. symmetricus* otoliths have been found in several southern California Pliocene and Pleistocene deposits, but they are not abundant in any of them

(Fitch, 1966, 1967, and unpublished data). The sagittae of a large, adult Pacific jackmackerel will exceed 10.0 mm in length.
*Material*: 1 otolith 4.3 mm long (Fig. 1w).

Sciaenidae—croakers

*Genyonemus lineatus* (Ayres)—white croaker

The white croaker ranges from Vancouver Island to Magdalena Bay, abounding in almost every type of habitat from the intertidal into depths of 600 feet. A near-record 14½-inch fish weighed 1.4 pounds. *G. lineatus* otoliths often are the most abundant fish remains in southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956), comprising 6,409 of the more than 11,000 otoliths recovered from the San Diego formation (Pliocene) near Imperial Beach (Fitch, unpublished data). The sagittae of a large, adult white croaker will exceed 12.5 mm in length.
*Material*: 8 otoliths from 4.5 to 7.0 mm long (Fig. 1x).

*Seriphus politus* Ayres—queenfish

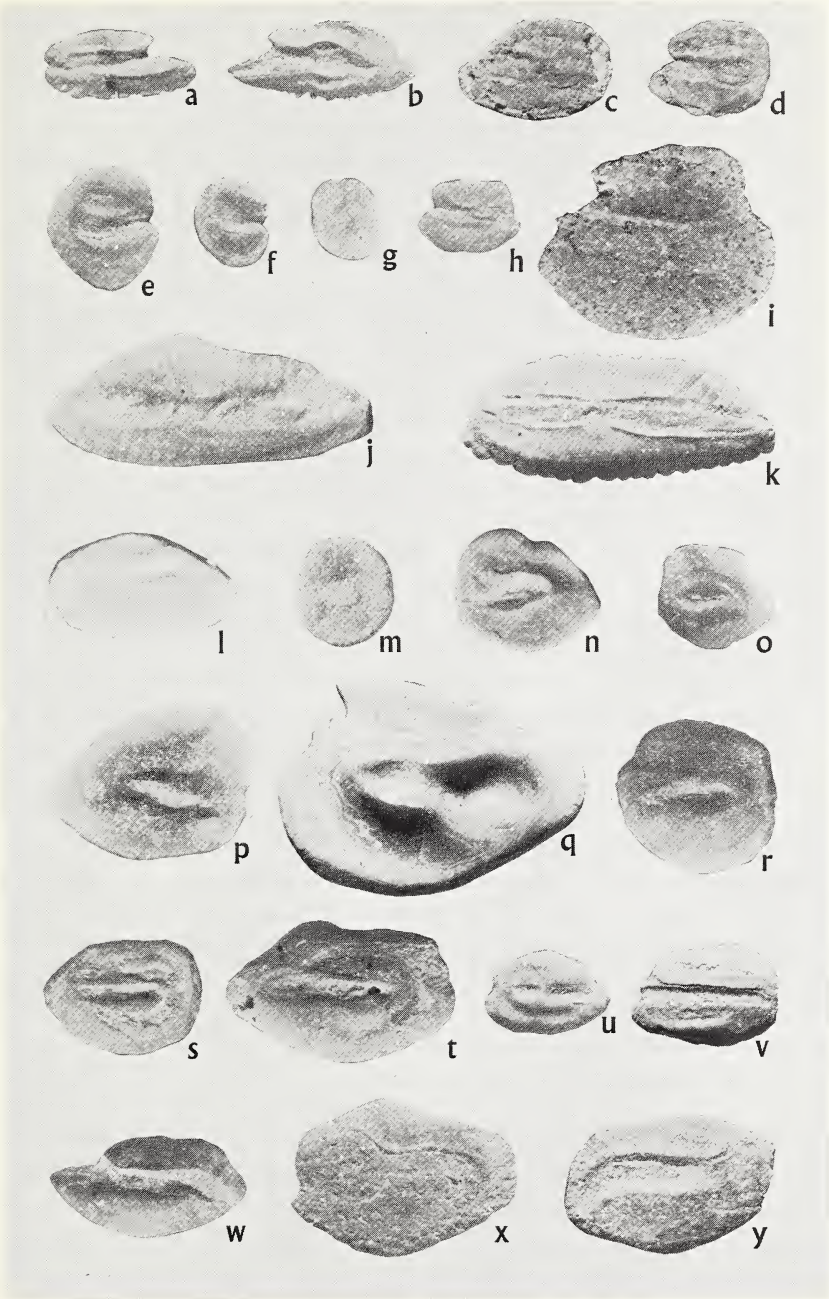
The queenfish ranges from Yaquina Bay, Oregon, to San Juanico Bay, Baja California, living in much the same habitat as the white croaker. A near-record 12-inch female weighed just over 10 ounces. *S. politus* otoliths have been found in many southern California Pliocene and Pleistocene deposits, often comprising a major portion of the total fish remains recovered (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956). The sagittae of a large, adult queenfish will exceed 10.0 mm in length.
*Material*: 8 otoliths from 3.0 to 6.6 mm long (Fig. 1y).

Embiotocidae—surfperches

*Cymatogaster aggregata* Gibbons—shiner perch

The shiner perch ranges from Port Wrangel, Alaska, to Santo Tomas Point, Baja California, being restricted to the mainland coast, primarily in

Figure 1. Teleost sagittae found in Timms Point silt at San Pedro, California. Lengths (in mm) are given for each otolith, and notations are made regarding its position in the skull (left or right), and condition if imperfect. a. *Clupea pallasi*, 3.3, *l*; b. *Engraulis mordax*, 4.1, *r*; c. *Ceratoscopelus townsendi*, 2.6, *r*, badly worn; d. *Diaphus theta*, 2.7, *r*; e. *Electrona rissoi*, 3.4, *l*; f. *Protomyctophum crockeri*, 1.7, *l*; g. *Stenobrachius leucopsarus*, 1.6, *l*; h. *Tarletonbeania crenularis*, 2.0, *r*; i. *Lampadena urophaos*, 4.0, *r*, anterior end missing; j. *Merluccius productus*, 10.2, *r*, posterior tip missing; k. *Theragra chalcogramma*, 9.8, *r*; l. *Melamphaes lugubris*, 1.3, *l*, badly eroded; m. *Scopelogadus bispinosus*, 2.0, *r*; n. *Citharichthys sordidus*, 4.5, *l*; o. *C. stigmaeus*, 2.7, *l*; p. *C. xanthostigma*, 6.3, *r*; q. *Atheresthes stomias*, 9.0, *l*, badly eroded; r. *Glyptocephalus zachirus*, 3.3, *r*; s. *Lyopsetta exilis*, 3.6, *r*; t. *Parophrys vetulus*, 5.0, *r*; u. *Microstomus pacificus*, 2.8, *l*; v. *Atherinops affinis*, 4.4, *r*, anterior tip missing; w. *Trachurus symmetricus*, 4.3, *r*, badly worn; x. *Genyonemus lineatus*, 5.0, *r*, badly worn; y. *Seriphus politus*, 6.6, *l*, badly worn. Photographs by Jack W. Schott.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depths shallower than 50 feet but sometimes caught as deep as 400. A record-sized pregnant female weighed just under 3 ounces. *C. aggregata* otoliths are abundant in most southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, and unpublished data; Fitch and Reimer, 1967), comprising 1,129 of the more than 2,700 otoliths recovered from a San Pedro Pleistocene deposit (Miraflores Street: Fitch, 1967). Bagg (1912) illustrated a *C. aggregata* sagitta from Timms Point, but did not identify it except as an otolith. The sagittae of a large, adult shiner perch will exceed 6.5 mm in length.
*Material*: 114 otoliths from 2.2 to 6.8 mm long (Fig. 2a).
Embiotocidae—unidentified surfperches

Seven otolith fragments in the Zinsmeister collection could be identified as belonging to family Embiotocidae, but it was impossible to assign them to a genus or species.

Labridae—wrasses

*Oxyjulis californica* (Günther)—señorita

The señorita ranges from Natural Bridges State Park, California, to Cedros Island, inhabiting shallow areas of rocky substrate where kelp beds and other vegetation grow. A near-record 9-inch male speared at Dana Point in January 1965 weighed 4 ounces. Señorita otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967, and unpublished data). The sagittae of a large, adult señorita will exceed 3.5 mm in length.
*Material*: 2 otoliths 1.5 mm long (Fig. 2b).

*Pimelometopon pulchrum* (Ayres)—California sheephead

The California sheephead ranges from Monterey Bay to and into the Gulf of California. Throughout much of this area they abound in rocky areas, particularly where dense kelp beds grow. The male sheephead grows bigger and lives longer than the female. A record weight seems to be 36¼ pounds, but this fish was not measured. A 29-pound male was 32 inches long. *P. pulchrum* remains, primarily jaw and pharyngeal teeth, have been found in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, and unpublished data; Kanakoff, 1956).
*Material*: 3 jaw teeth, plus 1 pharyngeal clump in the Zinsmeister collection.

Scorpaenidae—rockfishes

*Sebastodes goodei* Eigenmann and Eigenmann—chilipepper

The chilipepper ranges from Vancouver Island to Magdalena Bay, inhabiting depths of 350 to 1,080 feet when adult, but living in shallower water as a juvenile. A 20½-inch female (they are reported to attain 22 inches)

weighed 3 pounds 5 ounces. *S. goodei* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult chilipepper will exceed 17.0 mm in length.
*Material*: 1 otolith 7.3 mm long (Fig. 2d).

*Sebastodes hopkinsi* Cramer—squarespot rockfish

The squarespot rockfish ranges from Halfmoon Bay, California, to south of Ensenada, Baja California, usually in depths of 60 to 600 feet. They are reported to attain a size of 11 inches and about ½ pound. An 8½-inch fish weighed just over 4 ounces and was found to be 5 years old. *S. hopkinsi* remains have not been identified from any other fossil deposit. The sagittae of a large, adult squarespot rockfish will exceed 10.0 mm in length.
*Material*: 1 otolith 4.5 mm long (Fig. 2c).

*Sebastodes rosaceus* Jordan and Gilbert—rosy rockfish

The rosy rockfish ranges from Queen Charlotte Sound to Turtle Bay, Baja California, usually in 60 to 450 feet of water. A 10-inch female (the species attains a maximum of 12¾ inches) weighed slightly less than ½ pound. I have not identified *S. rosaceus* remains from any other fossil deposit. The sagittae of a large, adult rosy rockfish will exceed 13.0 mm in length.
*Material*: 1 otolith 8.7 mm long (Fig. 2e).

*Sebastodes* spp.—rockfishes, species undetermined

The otoliths of most of the 52 species of *Sebastodes* inhabiting the waters of California can be distinguished one from the other if they are from adult fish, and if they are not badly worn or broken. Such characters as length and shape of rostrum (if present), configuration of posterior end, presence or absence of marginal frills, angle of posterior taper, depth of sulcus, and number of growth zones (annuli) for otolith length are helpful for identifying sagittae of the various species or species-complexes. Unfortunately, very few fossil rockfish otoliths are well enough preserved to be identified to species. Bagg (1912) illustrated a *Sebastodes* sagitta from this deposit but did not identify it except as an otolith. Kanakoff (1956) reported *Sebastodes* otoliths from a Newport Beach Pleistocene deposit.
*Material*: 464 otoliths, apparently representing more than five species, mostly from juveniles.

*Sebastolobus* sp.—channel rockfish

Two species of *Sebastolobus* inhabit the waters off California: *S. alascanus*, which attains nearly 30 inches, lives in shallower depths (to 2,000 feet) than the smaller (15 inches maximum) *S. altivelis*, which has been caught as deep as 2,500 feet. *Sebastolobus* otoliths are readily distinguished from those of *Sebastodes*, but I have not found any characters (except size) to distinguish sagittae of *S. alascanus* from those of *S. altivelis*. Otoliths from a large (12-

inch) *S. altivelis* are about 10.0 mm long, whereas those from a large (21-inch, and 4¼-pound) *S. alascanus* are about 16.0 mm—both fish appeared to be roughly the same age.

*Material*: 3 otoliths from 7.0 to 9.0 mm long, the largest (Fig. 2f) probably from the shortspine channel rockfish, *S. alascanus* Bean.

Cottidae—sculpins

*Artedius notospilotus* Girard—bonehead sculpin

The bonehead sculpin ranges from Puget Sound, Washington, to Cape Colnett, Baja California, being taken in the intertidal and in 180 feet at the other extreme. A record-sized female trawled off Anaheim Bay, California, in February 1957, was 8¼ inches long and weighed just over 6 ounces. *A. notospilotous* otoliths have been found in several southern California Pliocene and Pleistocene deposits, but they are never abundant (Fitch, unpublished data; Fitch and Reimer, 1967). The sagittae of a large, adult bonehead sculpin will exceed 6.0 mm in length.

*Material*: 6 otoliths from 3.5 to longer than 5.3 mm, the length of a fragmented one (Fig. 2g).

*Chitonotus pugetensis* (Steindachner)—roughback sculpin

The roughback sculpin ranges from northern British Columbia to Magdalena Bay, usually at depths of 100 to 300 feet. A 7-inch fish, about maximum for the species, weighed just under 3 ounces. *C. pugetensis* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1967, and unpublished data). The sagittae of a large, adult roughback sculpin will exceed 6.0 mm in length.

*Material*: 7 otoliths from 2.6 to 4.4 mm long (Fig. 2h).

*Enophrys taurina* Gilbert—bull sculpin

The bull sculpin ranges from Monterey Bay to Santa Catalina Island, California, in depths of 30 to 800 feet (usually 100 to 250). A 6-inch fish, about maximum for the species, will weigh about 3 ounces. *E. taurina* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967 and unpublished data). The sagittae of an adult bull sculpin will exceed 5.5 mm in length.

*Material*: 6 otoliths from 4.4 to 5.2 mm long (Fig. 2i).

*Icelinus burchami* Evermann and Goldsborough—dusky sculpin

The dusky sculpin ranges from Alaska (55° N) to Santa Catalina Island, California (at least). It has been captured at depths of 600 to 1,500 feet, but appears to be rare throughout its range. A 5½-inch fish, about maximum for the species, weighs just over 2 ounces. *I. burchami* sagittae bear no resemblance to those of any other *Icelinus* otolith in my collection (six species), in fact

they are so different, they suggest a generic affinity other than with *Icelinus*. The dusky sculpin apparently was much more abundant in the Pliocene than it now is—nearly 600 of its otoliths were recovered from the Lomita marl at San Pedro (Fitch, unpublished data). The sagittae of an adult dusky sculpin will exceed 5.0 mm in length.
*Material*: 1 otolith 3.9 mm long (Fig. 2j).

*Icelinus filamentosus* Gilbert—threadfin sculpin

The threadfin sculpin ranges from northern British Columbia to the vicinity of Ensenada, at least. It is abundant on a muddy or sandy mud bottom in 60 to about 1,200 feet of water. A near-record 10½-inch female weighed just under 7 ounces. Otoliths of *I. filamentosus* have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult threadfin sculpin will exceed 10.0 mm in length.
*Material*: 7 otoliths from 3.6 to 5.7 mm long (Fig. 2k).

*Icelinus fimbriatus* Gilbert—fringed sculpin

The fringed sculpin ranges from about San Francisco to San Diego, having been taken in 150 to nearly 1,000 feet of water. An 8-inch female (maximum for the species is reported as 9 inches) weighed exactly 3 ounces. *I. fimbriatus* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult fringed sculpin will exceed 7.5 mm in length.
*Material*: 7 otoliths from 3.5 to 5.2 mm long (Fig. 2n).

*Icelinus quadriseriatus* (Lockington)—yellowchin sculpin

The yellowchin sculpin is one of the most abundant members of the family in moderate depths (50 to 250 feet) between about Point Reyes, California, and Cape San Lucas, Baja California. A 3½-inch fish, the largest of nearly 10,000 examined, weighed slightly less than 1 ounce. *I. quadriseriatus* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1966, and unpublished data). The sagittae of a large, adult yellowchin sculpin will exceed 3.8 mm in length.
*Material*: 43 otoliths from 2.4 to 4.1 mm long (Fig. 2 1).

*Icelinus tenuis* Gilbert—spotfin sculpin

The spotfin sculpin ranges from Queen Charlotte Sound to Guadalupe Island, Baja California, usually in depths of 100 to 400 feet. At maximum length, perhaps 4½ inches, a female *I. tenuis* probably weighs less than 1 ounce, even when full of roe. Spotfin sculpin otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967, and un-

published data). The sagittae of a large, adult spotfin sculpin will exceed 4.5 mm in length.
*Material*: 11 otoliths from 2.5 to 4.0 mm long (Fig. 2m).

*Leptocottus armatus* Girard—Pacific staghorn sculpin

The Pacific staghorn sculpin ranges from northwestern Alaska to San Quintin Bay, Baja California, being especially abundant in shallow outer coast waters, and in bays and lagoons. A 10-inch female (2 inches short of the reported maximum) netted in 1958, weighed ½ pound. *L. armatus* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967, and unpublished data; Kanakoff, 1956). The sagittae of an adult staghorn sculpin will exceed 9.0 mm in length.
*Material*: 3 otoliths from 4.2 to 5.8 mm long (2o).

*Malacocottus zonurus* Bean—blackfin sculpin

The blackfin sculpin ranges from the Gulf of Alaska to southern Washington, being relatively abundant in 90 to 500 feet. It is reported to attain 8 inches and 1/3 pound, but no data are available for a record-sized fish. *M. zonurus* otoliths have been found in only one other southern California fossil deposit (Lomita marl Pliocene, San Pedro)—more than 650 having been recovered from a relatively small field sample (Fitch, unpublished data). The sagittae of an adult blackfin sculpin will exceed 9.0 mm in length.
*Material*: 4 otoliths from 6.5 to 8.0 mm long (Fig. 2p).

*Radulinus asprellus* Gilbert—slim sculpin

The slim sculpin ranges from Kodiak Island, Alaska, to about Ensenada, being fairly abundant in 150 to 600 feet of water. A 5½-inch fish (large for the species) weighed about 1 ounce. Otoliths of *R. asprellus* have been found in several southern California Pliocene and Pleistocene deposits, over 1,300 having been recovered from the Lomita marl Pliocene at San Pedro (Fitch, 1967, and unpublished data). The sagittae of a large, adult slim sculpin will exceed 4.0 mm in length.
*Material*: 81 otoliths from 2.5 to 4.3 mm long (Fig. 2q).

Cottidae—genera and species undetermined

Cottid otoliths are easy to identify to family, but if they are worn or broken it is nearly impossible to assign a generic (except for *Icelinus*) or specific name. Most of the cottid otoliths in this deposit were badly eroded (perhaps from digestive action by some predator), and even though the majority of these appeared to be *Icelinus*, I preferred to list them simply as "undetermined cottids" for ease in accounting. Bagg (1912) illustrated two cottid sagittae from this deposit but did not identify them except as otoliths.
*Material*: 419 otoliths

Agonidae—poachers

*Xeneretmus* cf. *latifrons* (Gilbert)—blackedge poacher

The sagittae of the four species of *Xeneretmus* known to California are impossible to distinguish one from the other unless they are in perfect or near-perfect condition, and even then the task is difficult. Two of the species are rare, deep-water forms (*X. ritteri* and *X. leiops*), but the other two, *X. triacanthus* and *X. latifrons* are relatively common in moderate depths. *X. latifrons* is by far the most abundant of the four, and on this basis alone, I have questionably assigned the poacher otoliths from this deposit. The blackedge poacher ranges from southern British Columbia to about Ensenada, usually in 300 to 900 feet of water. A 7½-inch individual, which is apparently maximum length for *X. latifrons,* weighed slightly less than 1 ounce. *Xeneretmus* otoliths have been found in only one other southern California fossil deposit: Lomita marl Pliocene, San Pedro (Fitch, unpublished data). The sagittae of a large, adult blackedge poacher will exceed 5.0 mm in length.
*Material*: 2 otoliths, only one measurable (3.4 mm long, Fig. 2r).

Gobiidae—gobies

*Coryphopterus nicholsi* (Bean)—bluespot goby

The bluespot goby ranges from British Columbia to San Martin Island, Baja California, typically from the shallow subtidal into 200 feet or more. The maximum size attained by the species is about 5 inches and 1 ounce. *C. nicholsi* otoliths have been found in many southern California Pliocene and Pleistocene deposits, over 1,700 having been recovered from the Lomita marl Pliocene at San Pedro (Fitch, 1967, and unpublished data). The sagittae of a large, adult bluespot goby will exceed 3.0 mm in length.
*Material*: 276 otoliths from 1.1 to 3.5 mm long (Fig. 2s).

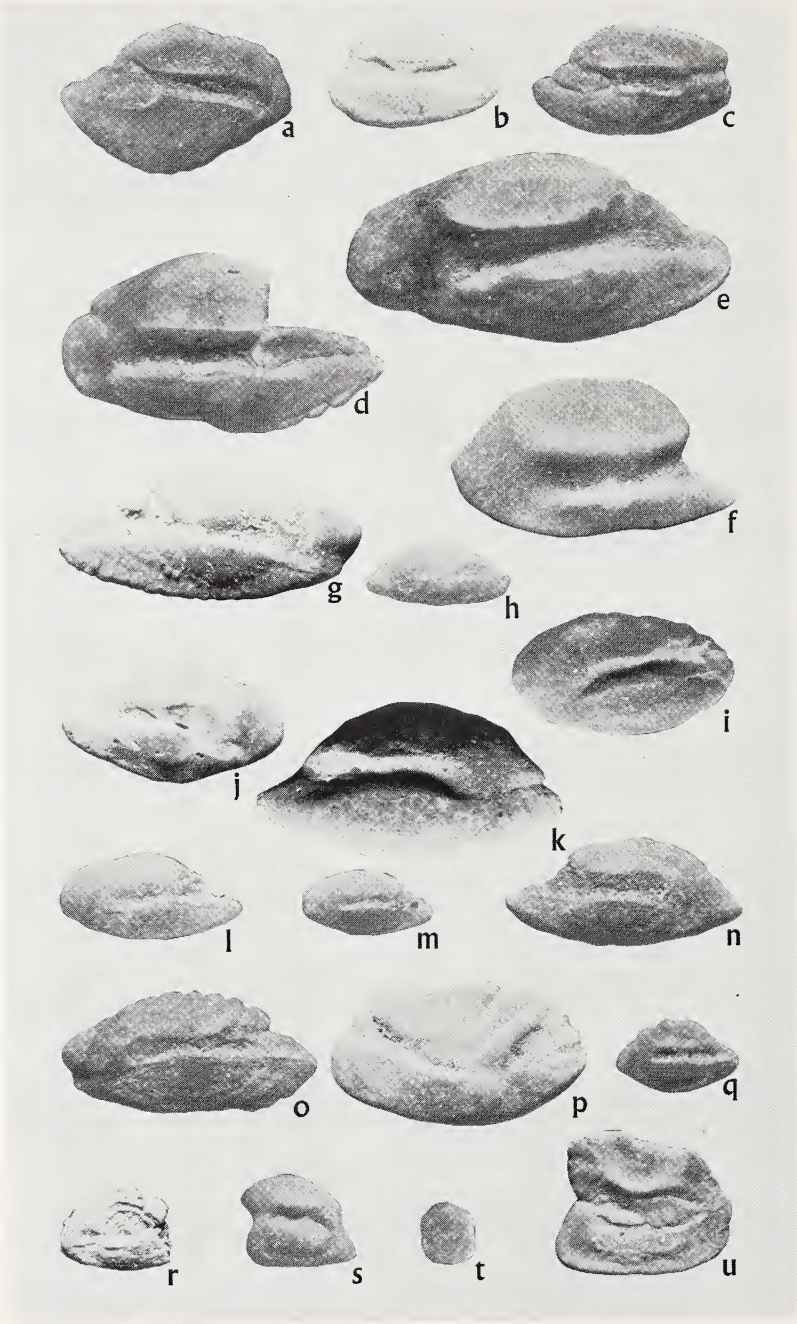
*Lethops connectens* Hubbs—halfblind goby

The halfblind goby ranges from Monterey Bay to about Cape Colnett, Baja California, but it is not very common north of Point Conception. Juveniles often have been observed in the water column in and around kelp beds, but adults are more secretive in their habits and usually remain hidden under rocks, in kelp holdfasts, and similar places. A large adult, slightly longer than 2 inches, will have sagittae longer than 1.4 mm. Otoliths of halfblind gobies have been found in a number of Pleistocene and Pliocene deposits in southern California (Fitch, unpublished data).
*Material*: 78 otoliths from 0.7 to 1.3 mm long (Fig. 2t).

Batrachoididae—toadfishes

*Porichthys notatus* Girard—plainfin midshipman

The plainfin midshipman ranges from southeastern Alaska to Cedros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Island, Baja California, being one of the half-dozen most abundant species trawled in 300 to 750 feet of water. A 13½-inch male (2 inches short of the reported maximum) weighed just over 14 ounces. *P. notatus* otoliths usually are abundant in southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, 1967, and unpublished data; Fitch and Reimer, 1967), nearly 700 having been recovered from the Lomita marl Pliocene at San Pedro (Fitch, unpublished data). The sagittae of a large, adult plainfin midshipman will exceed 10.0 in length.
*Material*: 101 otoliths from 1.5 to 6.0 mm long (Fig. 2u).

## Stichaeidae—pricklebacks

*Lyconectes aleutensis* Gilbert—dwarf wrymouth

The dwarf wrymouth ranges from the Bering Sea to Eureka, California, usually at depths of 150 to 1,200 feet or more. The species apparently attains a length of 12 inches and a weight of about 2 ounces. Otoliths of *L. aleutensis* have been found in several other southern California Pliocene and Pleistocene deposits, but they are not abundant in any of these (Fitch, unpublished data). The sagittae of a large, adult dwarf wrymouth will exceed 5.0 mm in length.
*Material*: 25 otoliths from 2.8 to 5.2 mm long (Fig. 3a).

## Zoarcidae—eelpouts

*Lycodopsis pacifica* (Collett)—blackbelly eelpout

The blackbelly eelpout ranges from the Gulf of Alaska to Ensenada (at least), being very abundant in trawl catches made in depths of 100 to 800 feet or more. The species is known to attain a size of 14 inches and nearly 1/3 pound. *L. pacifica* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967, and unpublished data). The sagittae of an adult blackbelly eelpout will exceed 5.0 mm in length.
*Material*: 34 otoliths from 2.7 to 4.8 mm long (Fig. 3b).

Figure 2. Teleost sagittae found in Timms Point silt at San Pedro, California. Lengths (in mm) are given for each otolith, and notations are made regarding its position in the skull, and condition if imperfect. a. *Cymatogaster aggregata*, 5.2, *r*; b. *Oxyjulis californica*, 1.5, *r*; c. *Sebastodes hopkinsi*, 4.5, *r*; d. *S. goodei*, 7.3, *l*; e. *S. rosaceus*, 8.7, *l*; f. *Sebastolobus* sp., 9.0, *l*, badly worn; g. *Artedius notospilotus*, 5.3, *r*; h. *Chitonotus pugetensis*, 3.2, *l*; i. *Enophrys taurina*, 5.0, *l*; j. *Icelinus burchami*, 3.9, *r*, badly eroded; k. *I. filamentosus*, 5.4, *r*, badly worn; l. *I. quadriseriatus*, 4.1, *l*; m. *I. tenuis*, 2.9, *l*; n. *I. fimbriatus*, 5.2, *r*; o. *Leptocottus armatus*, 5.8, *l*; p. *Malacocottus zonurus*, 8.0, *l*, badly worn; q. *Radulinus asprellus*, 2.8, *l*; r. *Xeneretmus* sp., 3.4, *l*, rostrum missing and badly eroded; s. *Coryphopterus nicholsi*, 2.8, *r*; t. *Lethops connectens*, 1.2, *r*; u. *Porichthys notatus*, 5.5, *r*. Photographs by Jack W. Schott.

Brotulidae—brotulas

*Brosmophycis marginata* (Ayres)—red brotula

The red brotula ranges from southeastern Alaska to Ensenada (at least), mostly in depths of 60 to 400 feet. Although reported to attain 18 inches, few individuals are seen that exceed 16 inches and 12 ounces. *B. marginata* otoliths have been found in several southern California Pliocene and Pleistocene deposits, but they are never abundant (Fitch, 1967, and unpublished data). The sagittae of a large, adult red brotula will exceed 14.0 mm in length.
*Material*: 15 otoliths from 1.4 to 5.8 mm long (Fig. 3c).

Ophidiidae—cusk-eels

*Otophidium taylori* (Girard)—spotted cusk-eel

The spotted cusk-eel ranges from about northern Oregon to San Cristobal Bay, Baja California, primarily in 60 to 800 feet of water. A near-record 14¼-inch specimen caught off San Pedro in 1960 weighed about 10 ounces. *O. taylori* otoliths are abundant in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956). The sagittae of a large, adult spotted cusk-eel will exceed 11.0 mm in length.
*Material*: 113 otoliths from 2.9 to 8.0 mm long (Fig. 3d).

Ammodytidae—sandlances

*Ammodytes hexapterus* Pallas—Pacific sandlance

The Pacific sandlance ranges from the Bering Sea to San Simeon, California, often occurring in schools from the surf zone to a considerable distance

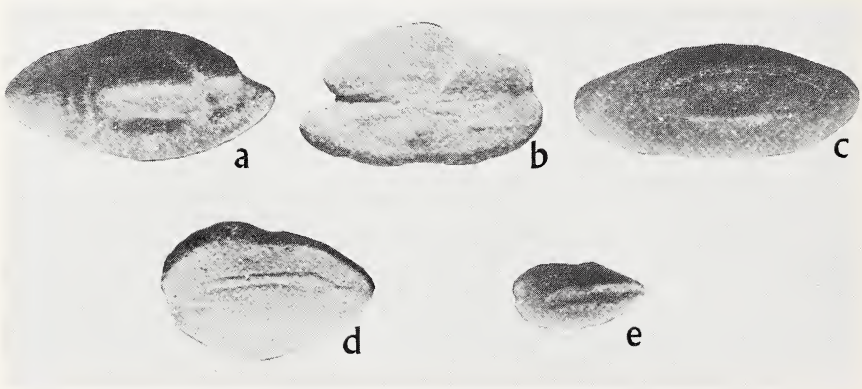


Figure 3. Teleost sagittae found in Timms Point silt at San Pedro, California. Lengths (in mm) are given for each otolith, and a notation is made as to whether it is left or right. a. *Lyconectes aleutensis*, 4.9, *l*; b. *Lycodopsis pacifica*, 4.4, *r*; c. *Brosmophycis marginata*, 5.2, *l*; d. *Otophidium taylori*, 5.6, *r*; e. *Ammodytes hexapterus*, 2.4, *l*. Photographs by Jack W. Schott.

offshore. The species is reported to attain a size of 8 inches and about ½ ounce. *A. hexapterus* otoliths have been found in several southern California Pliocene and Pleistocene deposits (Fitch, unpublished data). The sagittae of a large, adult Pacific sandlance will exceed 3.0 mm in length.
*Material*: 8 otoliths from 1.4 to 3.2 mm long (Fig. 3e).

Unidentified teleosts

Two otoliths (very badly worn), 8 teeth, 121 vertebrae, and 1 fin spine recovered from this deposit could not be identified except as teleost remains. Most of these are presumed to have come from the same species that "left" their otoliths.

## DISCUSSION

Nine of the more than 53 species of teleosts identified from the Timms Point silt belonged to two families of mesopelagic fishes (Myctophidae and Melamphaidae) that seldom are captured in depths shallower than about 1,000 feet. All of these are found in waters offshore from San Pedro as well as at latitudes to the north and south of this fossil deposit, and all but one, *Electrona rissoi*, are taken abundantly in midwater trawls. It is commonplace to find otoliths of one to three species of myctophids in southern California Pliocene and Pleistocene deposits, including those presumably laid down at relatively shallow depths (±60 feet), but few deposits that I have investigated have contained melamphaid otoliths, or sagittae from as many myctophid species (7) as I found at this locality.

Otoliths of deep-sea fishes can arrive in moderately-deep or shallow deposits in any of several ways: (i) fishes can be eaten by a predator in deeper waters and their otoliths transported to a shallow area in the predator's digestive tract, which they can pass through in a relatively unaltered condition; (ii) when mass mortalities occur, the dead fishes can be transported to shallower areas by currents or wind action, or in the stomachs of scavengers; (iii) mesopelagics which undertake diurnal migrations are known to approach close to shore at night near the heads of submarine canyons or where the bottom gradient rises abruptly near shore—predation and mortality in these shallow waters will result in otoliths being deposited there; (iv) spawning migrations take some species into shallower waters than they inhabit the rest of the year; and (v) deep areas which contain otoliths of offshore species can be folded or faulted upward so that subsequent otolith deposition will be from shallow species (downfaulting of shallow bottom areas could also result in an admixture of otoliths from nearshore and offshore species).

Six of the 53 teleost species found in this deposit (*Ammodytes, Atheresthes, Lyconectes, Malacocottus, Microgadus,* and *Theragra*) have not been captured or noted south of about Monterey, California, during modern times (Figure 4). Only two of these (*Ammodytes* and *Microgadus*) are found in

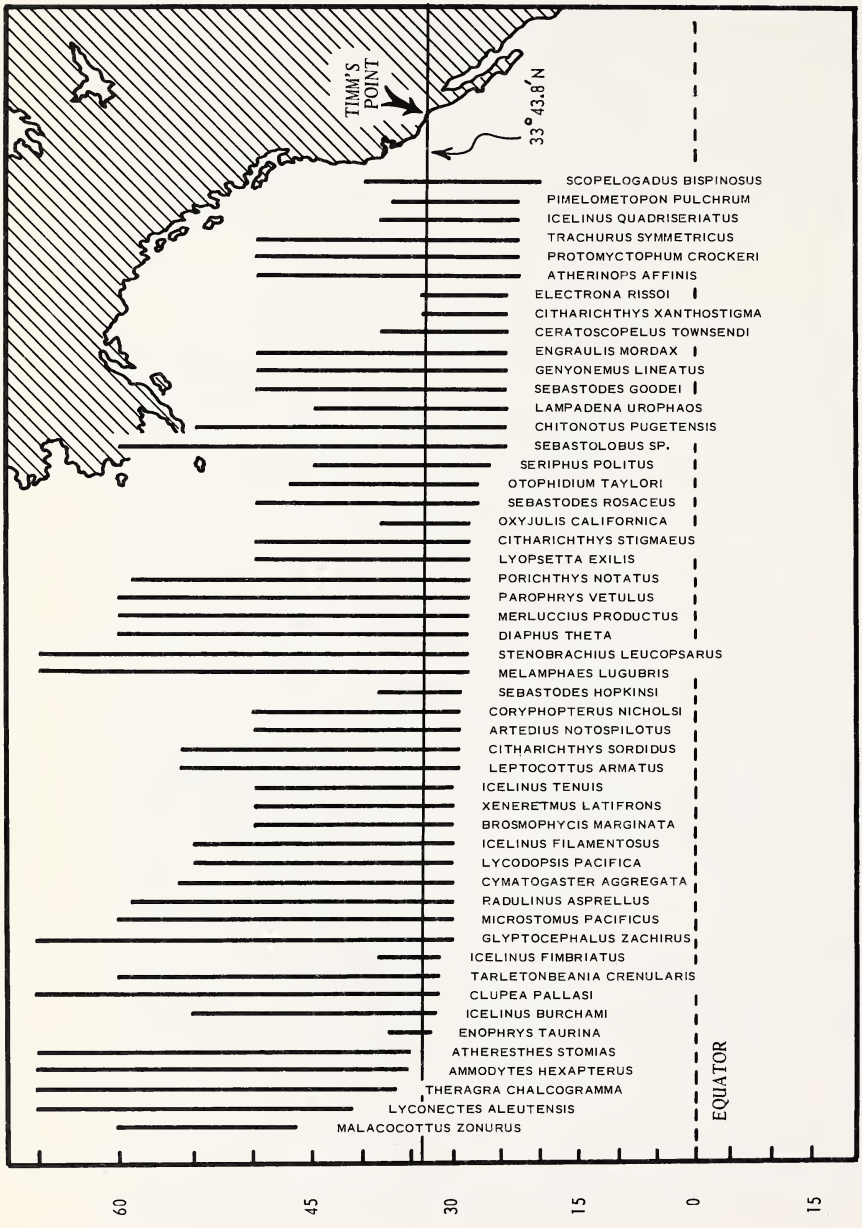


Figure 4. Present-day distributions of 51 of the 53 species of teleosts identified from Timms Point silt at San Pedro, California (lat. 33° 43.8′ N.). Otoliths of *Lethops connectens* (Monterey Bay to Cape Colnett) and *Microgadus proximus* (Alaska to Morro Bay) were identified after this chart was completed.

relatively shallow water, but even these species are more abundant in offshore waters where depths exceed 100 feet.

Only 10 of the more than 53 species identified from this deposit were captured during 3 years of beach seining (451 hauls) along the southern California coast to depths of about 10 or 12 feet (Carlisle, Schott, and Abramson, 1960), but 7 of these 10 were also taken during otter-trawling operations in Santa Monica Bay using fine-mesh nets in 60 to 600 feet. In all, these otter-trawling operations captured 27 of the 53+ Timms Point species (Calif. Dept. Fish and Game unpublished data). Obviously the Timms Point fish fauna admirably supports the statement of Valentine (1961) and others that deposition occurred at depths between 25 and 100 fathoms at a time when water temperatures were considerably cooler than at present.

In view of the numbers of northern fishes (Figure 4, Table 1), it would be interesting to know how many individuals of a given species are needed in a square mile of ocean before an otolith of that species finds its way into a given area of bottom. If such data were available, it would be possible to speculate as to the density of *Lyconectes aleutensis* that resulted in 25 of their otoliths being found in the 1,000 pounds or so of fossiliferous matrix that was examined. It would also be interesting to know if the single arrowtooth flounder otolith would represent a comparable number of *Atheresthes stomias*. It seems reasonable to assume that otoliths of a prey species or potential prey species (e.g., *Ammodytes* and *Lyconectes*) will be present in greater numbers than those of a large predator (e.g., *Atheresthes*) which would have few natural enemies. Unfortunately, as has been pointed out by a multitude of investigators, fossil deposits represent only death associations, so conclusions as to life associations must be relegated to the realm of pure speculation unless accompanied by irrefutable proof. Such proof is lacking in the present case.

## ACKNOWLEDGMENTS

This study was made possible by research grants (GB-1244 and GB-6490) from the National Science Foundation. In addition, many individuals were helpful in an assortment of ways. Richard A. Fitch washed, screened, and sorted the bulk of about 1,000 pounds of fossiliferous Timms Point silt that had been collected by numerous students and volunteer workers during Museum field trips supervised by George P. Kanakoff, then Curator of Invertebrate Paleontology, Los Angeles County Museum of Natural History. Dr. Charles R. Wright, Sanger, California, sent many otoliths that he had found in material from this site. Dan Gotshall, California Department of Fish and Game, Eureka; Richard B. Grinols, U.S. Bureau of Commercial Fisheries, Seattle; Robert J. Lavenberg, Los Angeles County Museum of Natural History; and S. J. Westrheim, Fisheries Research Board of Canada, Nanaimo, B.C., sent me otoliths from living species that were critical in identifying some com-

ponents of this fauna. Jack W. Schott, San Pedro, took the excellent otolith photographs; Walter Thomsen, Carmichael, produced the fish distribution map; and Mrs. Loretta Morris, San Pedro, typed the manuscript and its revisions.

The several student volunteers who excavated the deposit were: Nick Furjanick, Pat LaFollett, Louis Marinkovich, Peter Oringer, Robert Rashkin, Roger Reimer, and William Warner.

My wife, Arline, listened to my reading of the manuscript to see if it sounded satisfactory, and proofread various typed and printed versions.

To all these I offer my sincere thanks. If I have forgotten to mention anyone who helped bring this study to a successful conclusion, it has not been intentional.

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# OCCURRENCE OF A GIANT BISON, *BISON LATIFRONS*, AND A SLENDER-LIMBED CAMEL, *TANUPOLAMA*, AT RANCHO LA BREA

*By* WADE E. MILLER

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*Editor*

# OCCURRENCE OF A GIANT BISON, *BISON LATIFRONS*, AND A SLENDER-LIMBED CAMEL, *TANUPOLAMA*, AT RANCHO LA BREA

*By* Wade E. Miller[1]

Abstract: *Tanupolama* is recognized as a new constituent in the Rancho La Brea fauna. A previously overlooked record of *Bison latifrons* is confirmed by additional material and its association with *Bison antiquus* is noted for the first time. The geographic range of the former species of *Bison* is extended to southern California and its chronologic range into later Wisconsin time.

## Introduction

Despite the fact that the Rancho La Brea fauna is widely known, the richness of its contents has not yet been fully evaluated. In using this collection for comparative purposes, it was found that a specimen belonging to a camel other than the only heretofore identified species, *Camelops hesternus,* is present (Webb, 1965; Stock, 1963, p. 44). Although Stock (1963, p. 47-48) indicated that the only bison in the fauna is a moderate-sized species, *Bison antiquus*, a few elements of an extremely large bison are also in evidence. Additional species, even of large vertebrates, may yet be discovered in this extensive accumulation of Pleistocene life.

## Acknowledgments

Study of the Rancho La Brea collection at the Los Angeles County Museum of Natural History was made possible by the kind permission of Drs. Theodore Downs, Chief Curator of Earth Sciences, and J. R. Macdonald, Senior Curator of Vertebrate Paleontology. Thanks are due to Dr. Hildegarde Howard, Research Associate at the Los Angeles County Museum of Natural History, for encouraging the writing of this article.

## Discussion of Taxa

### **Tanupolama** Stock, 1928

The recognition of *Tanupolama*, a slender-limbed camel, in the Rancho La Brea collection is based on a complete adult astragalus, Los Angeles County Museum of Natural History (LACM) No. Z 2717 (Fig. 1). Maturity is indicated by the clear definition of processes and ridges and the noncancellous exterior. This specimen is 59.2 mm in greatest length, 35.7 mm in greatest width across the proximal ginglymi and 39.5 mm in greatest width across the distal ginglymi. These dimensions are significantly smaller than the smallest

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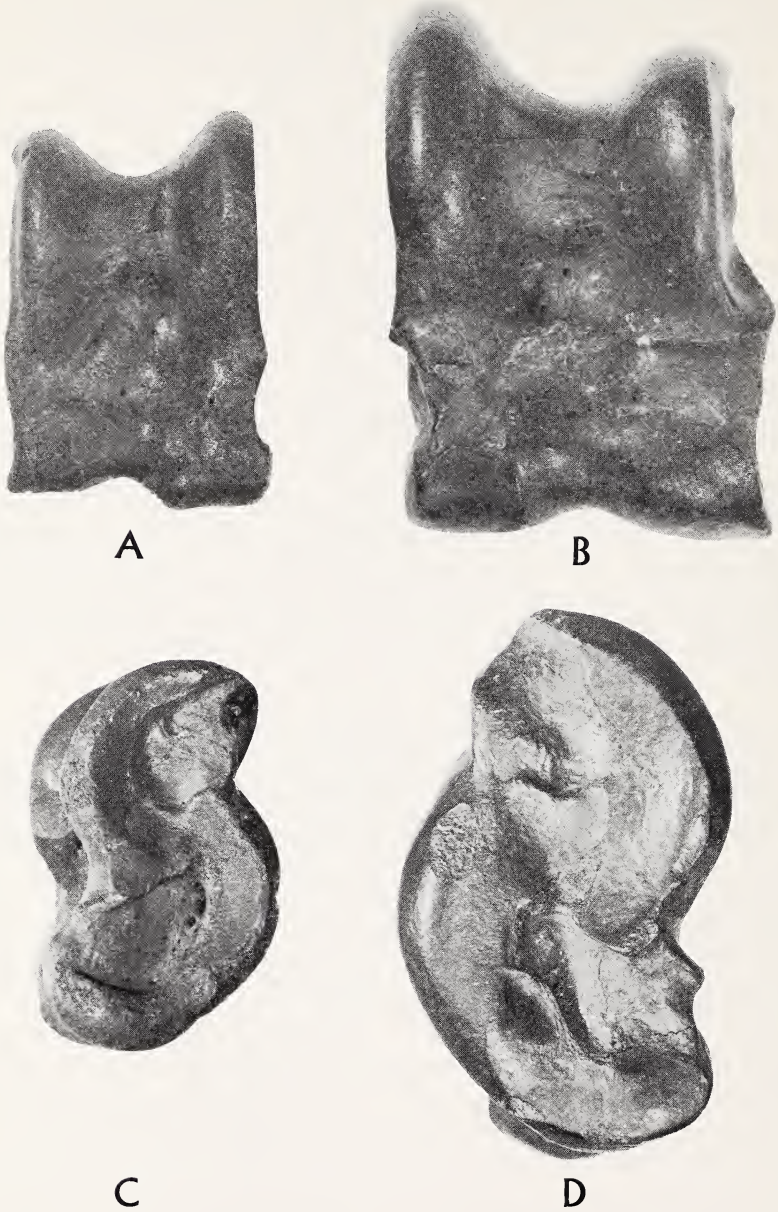


Figure 1. Comparison of camel astragali from Rancho La Brea. A, *Tanupolama*, anterior view. B, smallest adult *Camelops*, anterior view. C, *Tanupolama*, lateral view. D, smallest adult *Camelops*, lateral view. Scale 1½ x.

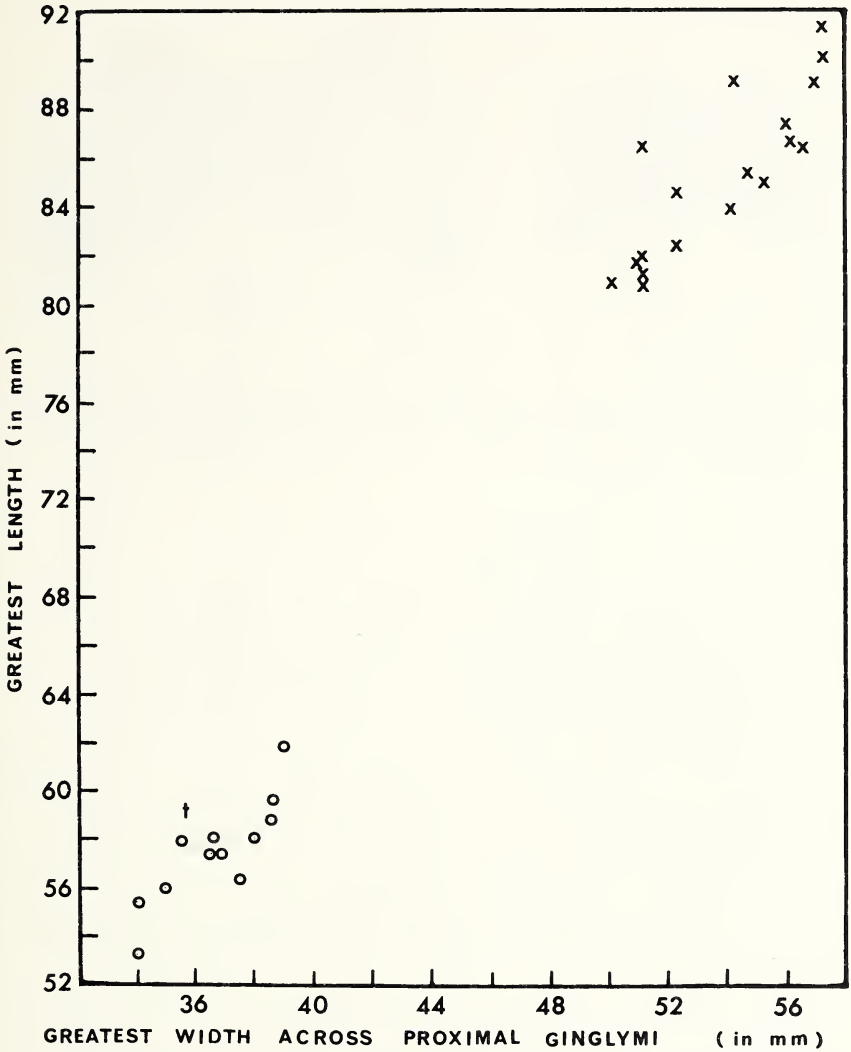


Figure 2. Scatter diagram of camel astragali. x = *Camelops* from Rancho La Brea; o = *Tanupolama* from McKittrick; t = *Tanupolama* from Rancho La Brea.

adult *Camelops* astragalus in the Rancho La Brea collection (Figs. 1 and 2), and even much smaller than the smallest juvenile observed. However, they are well within the range of those noted for *Tanupolama* from McKittrick, California (Fig. 2), the locality of the genotypic species. The only other genus of

camel recognized in post-Blancan deposits of North America is *Titanotylopus* (Webb, 1965, p. 44-45). This camelid is larger than *Camelops* and greatly exceeds *Tanupolama* in size (Barbour and Schultz, 1934, p. 291).

In the field notes taken by Wyman (1914, p. 50) during the excavations of the Rancho La Brea deposits, he states that the skull of a new camel was found, llama-like in structure. No further mention of the specimen was made, nor can any trace of it be found now in the collection. With the possible exception of proboscidean specimens, almost all the material from the pit of discovery (Pit 9) was unrecoverable due to ground water saturation. Possibly the specimen was never collected. The astragalus of the camel here identified as *Tanupolama* was recovered from this same pit near the location given for the skull. It occurred below a wood sample which was dated in excess of 40,000 years B.P. (Berger and Libby, 1966, p. 492).

Slaughter (1966, p. 86), in a table indicates the presence of *Tanupolama* at Rancho La Brea. He (1967, pers. comm.) has informed me, however, that this location was inadvertently listed and that the referred material came from the McKittrick deposits.

### **Bison latifrons** (Harlan, 1825)

Wyman (1926) listed the fossils that had been recovered at Rancho La Brea and discussed the presence of a skull (p. 32) of *Bison latifrons* whose horn-cores measured a "full six feet from tip to tip." According to Skinner and Kaisen (1947, p. 205-206), *B. latifrons* is the only species of *Bison* with a horn-core spread this great. Unfortunately, the skull reported by Wyman disintegrated upon removal. Whether any of the fragments were saved is not known. In the Rancho La Brea field notes (p. 66), Wyman states that two metapodials of a very large bison were collected. These elements, as well as the skull, were taken from Pit 9. The only bison element that I have seen from this pit is the distal one-third of a metatarsal, LACM No. Y 2557. Its proportions exceed those of any others seen in the Rancho La Brea collection and the specimen probably is assignable to the species *B. latifrons* (greatest mediolateral width at distal end, 87.0 mm; greatest anteroposterior thickness at distal end, 51.0 mm).

A few *Bison latifrons* bones are apparently also present in the material recovered from Pit 4. Its occurrence here marks the first time this species of *Bison* has been reported associated with *Bison antiquus* (no positive identification has been made of *B. antiquus* in Pit 9). Of further interest are the radiometric dates extracted from bone samples taken with these specimens from Pit 4, of 26,700 years B.P. at an eight foot depth and 28,000 years B.P. at a 15.5 foot depth (unpublished data currently being compiled at the UCLA Radiocarbon laboratory). This extends the chronologic range of *B. latifrons* into very late Wisconsin time. Material representing this species was recovered from a depth of ten to fifteen feet in Pit 4; *Bison antiquus* specimens have been

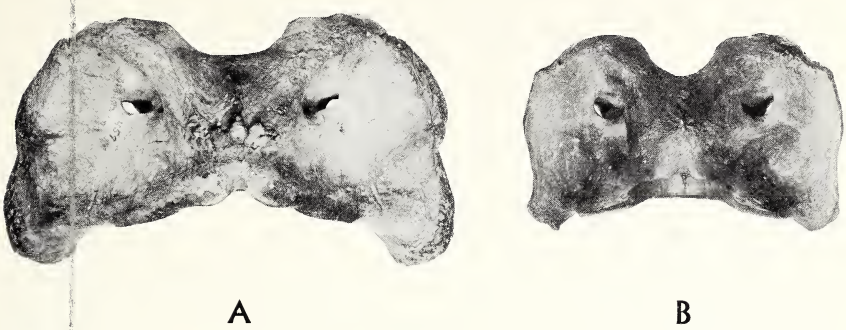


Figure 3. Comparison of bison atlases from Rancho La Brea, dorsal view. A, *Bison latifrons*. B, *Bison antiquus* (large specimen). About ½ x.

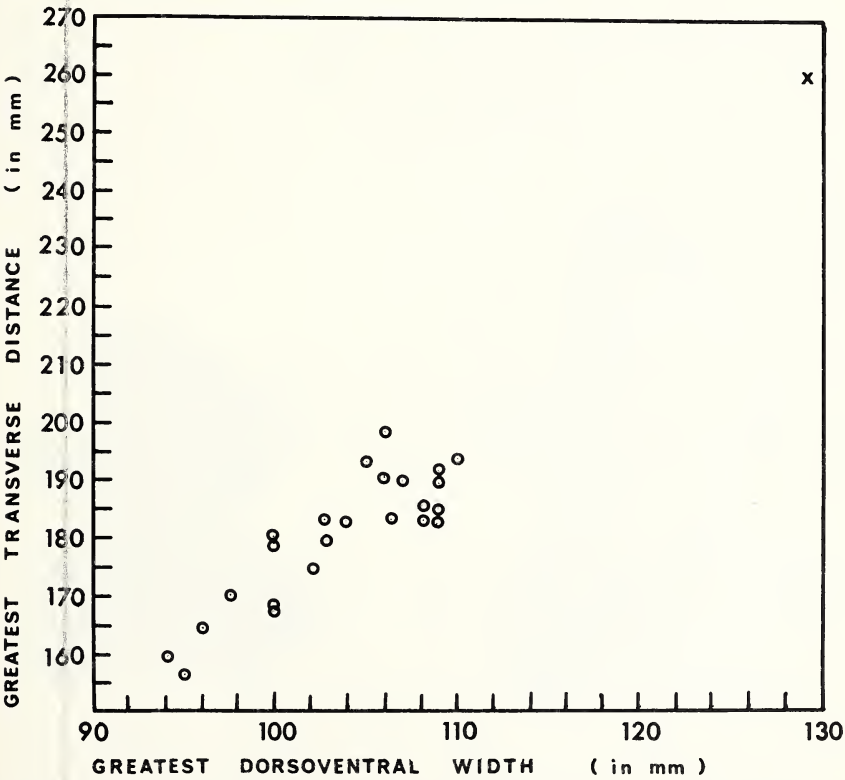


Figure 4. Scatter diagram of bison atlases from Rancho La Brea. o = *Bison antiquus*; x = *Bison latifrons*.

## TABLE 1

Skeletal measurements of *Bison latifrons* from Rancho La Brea

| | mm |
|---|---|
| Atlas (Y 6737) | |
| Greatest width across wings | 260 |
| Greatest dorsoventral thickness (across tubercles) | 131 |
| Greatest transverse distance (across proximal articulating surface) | 152 |
| Axis (Y 6734) | |
| Greatest length of centrum (including dens) | 148 |
| Greatest width (across anterior articulating surface) | 138 |
| Greatest width of dens | 059 |
| Height of neural spine (superior border of neural arch to tip of spine) | 124 |
| Scapula (Y 6738) | |
| Greatest anteroposterior distance (across articular surface) | 090 |
| Greatest transverse distance (across articular surface) | 075 |
| Ulna (Y 6736) | |
| Greatest anteroposterior distance (through anconeus process) | 126 |
| Height of olecranon process (above sigmoid notch) | 160 |
| Mandible (Y 6710) | |
| Length of jaw (lateral border of C/1 alveolus to angle) | 468 |
| Depth of jaw (at anterointernal border of P/2 alveolus) | 060 |
| Depth of jaw (at posterointernal border of M/3 alveolus) | 095 |
| Length of premolar series (from alveolar borders) | 068 |
| Length of molar series (from alveolar borders) | 115 |

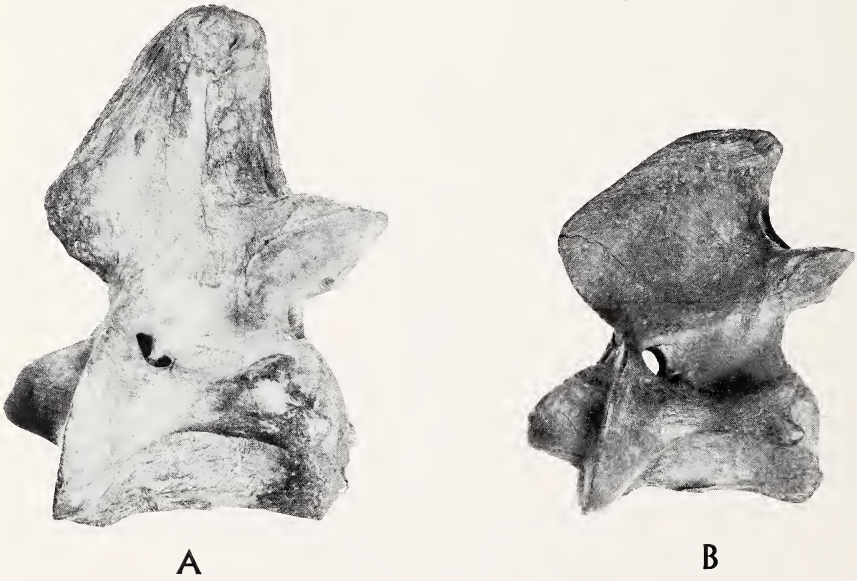


Figure 5. Comparison of bison axes from Rancho La Brea, lateral view. A, *Bison latifrons*. B, *Bison antiquus* (large specimen). About ½ x.

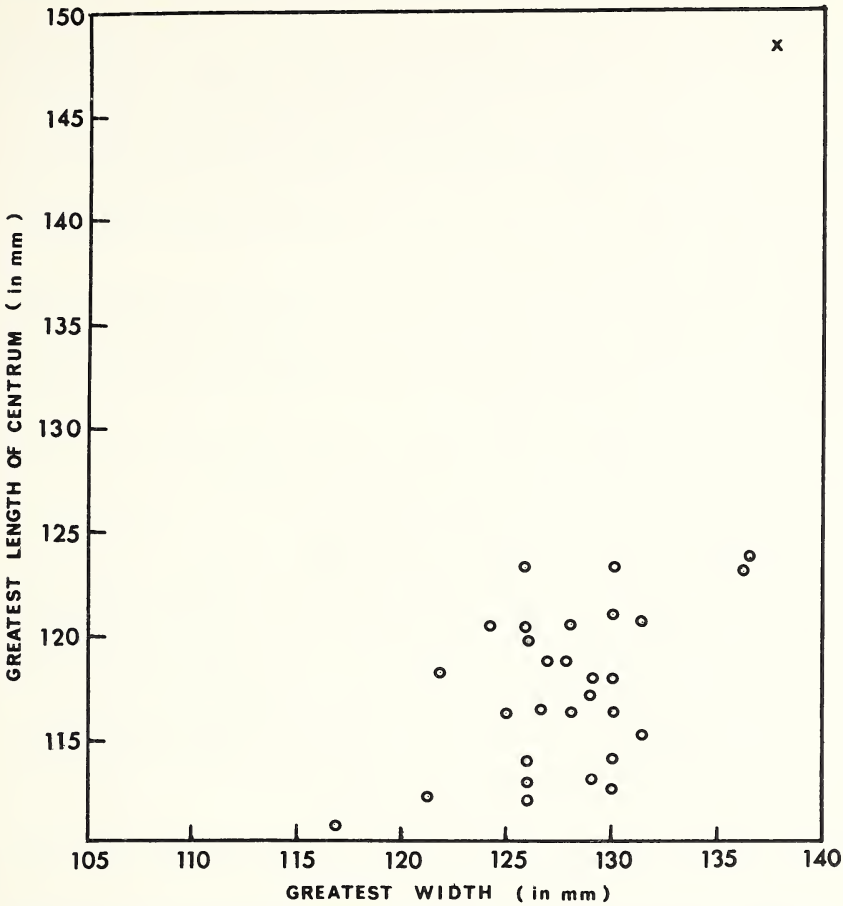


Figure 6. Scatter diagram of bison axes from Rancho La Brea. o = *Bison antiquus*; x = *Bison latifrons*.

taken from above and below this level. This record of the giant species of *Bison* now extends its geographic range to southern California. The first California record was reported by VanderHoof (1942) who described a complete skull from the northern part of the state. Savage (1951, p. 284) mentioned the presence of *B. latifrons* in Contra Costa County, California.

Recovered specimens from Pit 4 include an atlas, LACM No. Y 6737; an axis, LACM No. Y 6734; the proximal end of an ulna, LACM No. Y 6736; and a complete mandible, LACM No. Y 6710. All these specimens greatly exceed corresponding ones of *B. antiquus* in size and two show differences in proportions, the atlas and the axis (Figs. 3 and 5 and Table 1).

*Atlas.* This element far surpasses the equivalent one of *Bison antiquus* in size and further differs by being more rugose, possessing more massive ventral and dorsal tubercles and having a tendency toward a trapezoidal rather than a rectangular form (dorsal and ventral view). The present atlas was found to be identical to the corresponding element in *B. latifrons* specimens in the University of California Museum of Paleontology and the Los Angeles County Museum of Natural History collections. It is a little larger than the one of *Bison latifrons* and distinctly larger than that of *B. crassicornis* reported by Allen (1876, p. 14).

*Axis.* Like the atlas, this cervical vertebra is much larger than any similar element of *B. antiquus* in the Rancho La Brea fauna. It further differs by possessing a greater rugosity and a larger neural spine whose anterior edge is more steeply inclined (Fig. 5). The axis is indistinguishable from axes of *B. latifrons* used in comparison.

*Scapula.* The portion of this element available indicates a much larger bone but one whose proportions are similar to *B. antiquus.*

*Ulna.* Like the scapula, the proximal portion of the ulna compares favorably in shape to *Bison antiquus* but is much larger.

*Mandible.* The greater size of this element distinguishes it from lower jaws of *B. antiquus.* However, the teeth are relatively smaller, being about equal in size to many observed specimens of the smaller species. This observation was also made by VanderHoof (1942, p. 11); the complete jaw described by him is almost identical in size to the Rancho La Brea specimen.

Based on their large size, several postcranial juvenile specimens from Pit 3 of the Rancho La Brea deposits could possibly represent *Bison latifrons.*

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# RECORDS OF BATS FROM COSTA RICA

*By* ANDREW STARRETT AND RICHARD S. CASEBEER

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Dorothy M. Halmos
*Editor*

# RECORDS OF BATS FROM COSTA RICA

*By* Andrew Starrett[1] and Richard S. Casebeer[2]

Abstract: Twenty-five species of bats from Costa Rica are reported, ten species and one subspecies of which are new records for the country. Information on distribution patterns and ecological observations are included. New to the chiropteran fauna of Costa Rica are: *Saccopteryx leptura, Peropteryx macrotis, Pteronotus davyi, Chilonycteris psilotis, Micronycteris schmidtorum, Chrotopterus auritus, Mesophylla macconnelli, Natalus stramineas, Myotis simus, Myotis chiloensis* and *Eptesicus furinalis gaumeri. Balantiopteryx plicata* is reported from Costa Rica for the first time since the type description, and the separate generic status of *Mesophylla macconnelli* is reaffirmed.

## Introduction

In 1962, the Los Angeles County Museum of Natural History (LACM) was awarded a four-year grant from the U.S. Army Medical Research and Development Command to support a survey of the mammals and mammalian ectoparasites of Costa Rica. The mammals collected during the three years of the field phase of this study, and specimens collected in 1957 (Starrett and De la Torre, 1964), 1959, and 1961 (Casebeer, Linsky and Nelson, 1963, and Tamsitt and Valdivieso, 1961) by various field parties from the University of Southern California and the Los Angeles County Museum of Natural History, have provided this museum with a good representation of the chiropteran fauna of Costa Rica. Using this material as a nucleus, the LACM has been attempting to put together a picture of the distributional patterns of the bats of Costa Rica, with the aid of published records and specimens available in other collections, as well as continued collecting in that country. There are now known from Costa Rica at least 78 species of bats, based on authenticated published records and specimens reported in this paper, and the total number may be expected reasonably to reach 100 as the various collections continually being made by this museum and other institutions are worked up. An increase in interest in Neotropical bat faunas is represented by a number of recent publications which have included records of species from Costa Rica (in addition to those already cited): Carter, Pine and Davis, 1966; Davis, 1965 and 1966; Davis and Carter, 1962; Davis, Carter and Pine, 1964; Nelson, 1965; Walton, 1963. This paper reports on 226 specimens of 25 species of bats, ten species and one subspecies of which are new records for Costa Rica.

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Localities are listed after capitalized province names which are reported in alphabetical order. Elevations have been converted to meters for the sake of uniformity and ease of comparison; (when shown in italics, they represent reasonable estimates, usually based on topographic maps). Measurements are in millimeters and are for adult specimens unless otherwise indicated. Capitalized Forest Formations are those of L. R. Holdridge, from Slud, 1964.

## SPECIES OF BATS

### **Rhynchonycteris naso** (Wied-Neuwied)

*Vespertilio naso* Wied-Neuwied, 1820, Reise nach Brasilien in den Jahren 1815-1817, 1: 251, footnote.

*Rhynchonycteris naso,* Peters, 1867, Monatsb. preuss. Akad. Wiss., Berlin, p. 478.

*Specimens*: GUANACASTE: Río Colorado at Hacienda La Norma (Finca Coyolar) 5 km N, 4 km W Liberia, *50 m,* 3 ♂♂, 11 ♀♀; 0.8 miles by road SW Tilarán, (Santa Rosa drainage), 500 m, 1 ♂; Río Diria at Santa Cruz, 60 m, 1 ♂, 2 ♀♀; Sámara, sea level, 1 ♂. HEREDIA: 4 miles W Puerto Viejo de Sarapiquí, 92 m, 1 ♀ (TCWC). LIMON: Río Madre de Dios, near Finca La Lola, 50 m, 1 ♂. PUNTARENAS: 6.5 miles N, 2 miles W Puntarenas, 30 m, 1 ♂ (TCWC); Río La Vieja on Interamerican Highway, 110 m, 1 ♀; Boca de Barranca, sea level, 4 ♀♀; 2.8 miles E Golfito, 60 m, 1 ♂; 8 miles ENE Golfito, 30 m, 1 ♀; Rincón de Osa, headquarters area Osa Productos Forestales, 10 m, 1 ♂.

*Measurements*: Forearm, averages and ranges for 7 males and 12 females, respectively, 35.8 (34.5-37.3), 37.7 (36.3-38.8).

*Remarks*: Although this bat is known from every Middle American country and most tropical countries in South America (Sanborn, 1937), all previous Costa Rican records are based on 10 specimens, without locality, which were collected by G. K. Cherrie and cited first (as 11 specimens) by J. A. Allen (1897). The 30 specimens recorded here were all collected at low elevations (up to 500 m) and from localities which include both the driest and wettest regions of the country as well as both Pacific and Caribbean lowlands. All of the collecting localities, with the exception of that at Rincón de Osa, are in areas which have been modified ecologically by one type of agricultural use or another; the virgin tropical wet forest of the Rincón area is undergoing change due to investigatory lumber operations. The only immediately apparent ecological preference shown by *Rhynchonycteris* in Costa Rica is for watercourses. The series from Hacienda La Norma was collected during the day from two adjacent colonies hanging from the face of cliffs along the Río Colorado, the larger of the two colonies having an estimated 45 individuals, some of which were females carrying young. All the other LACM specimens were netted or shot over or next to streams or rivers along which they were hunting. They were taken variously in association with *Saccopteryx bilineata,*

*Noctilio leporinus, Noctilio labialis, Chilonycteris parnellii, Molossus* sp., and various stenodermines which used the watercourses as flyways.

### **Saccopteryx leptura** (Schreber)

*Vespertilio lepturus* Schreber, 1774, Die Saugethiere, Teil 1, Heft 8, pl. 57 (name); 1775, *ibid.*, Teil 1, Heft 9, pp. 173-174 (description).

*Saccopteryx lepturus,* Illiger, 1811, Prodromus systematis mammalium et avium, p. 121.

*Specimens*: GUANACASTE: Playas del Coco, sea level, 1 ♀; Mojal de Santa Cruz, Arenal (Cartajena), 55 m, 6 ♂♂, 2 ♀♀. LIMON: "El Tigre," approximately 14 km S Siquirres, 825 m, 1 ♀. PUNTARENAS: 15 km SE Jaco, Batalla's Finca, Esterillos Oeste, sea level, 1 ♀; 3.8 miles NW Villa Neilly along Interamerican Highway, *55 m,* 1 ♀; Rincón de Osa, headquarters area Osa Productos Forestales, 10 m, 1 ♂.

*Measurements*: Averages and ranges: forearm, 7 males, 5 females, respectively, 38.4 (37.0-39.6), 40.9 (39.8-42.5); (cranial, males and females together) greatest length of skull (6 specimens), 13.5 (13.2-13.8); condylocanine length (7), 11.8 (11.5-12.3); length of maxillary toothrow, C-$M^3$ (8), 5.2 (4.9-5.6); postorbital constriction (8), 2.2 (2.0-2.6); zygomatic breadth (7), 8.6 (8.5-9.1); mastoid breadth (7), 7.3 (7.1-7.5).

*Remarks*: This species was known previously in Middle America from Panama (Sanborn, 1937; Handley, 1966), Nicaragua (Davis *et al.*, 1964), El Salvador (Burt and Stirton, 1961) and Chiapas, Mexico (Carter *et al.*, 1966). The 13 specimens included here represent the first records of *S. leptura* from Costa Rica. All were collected at low elevations: the one from "El Tigre" represents the only record from the Caribbean slope and is from the highest elevation (825 m); the others are all from elevations below 60 m on the Pacific lowlands. These specimens were shot at night over roads or clearings or taken during the day from roosting sites in caves (Playas del Coco) or on sheltered areas of tree trunks (Mojal de Santa Cruz).

### **Peropteryx macrotis macrotis** (Wagner)

*Emballonura macrotis* Wagner, 1843, Arch. Naturgesch., Jahrg. 9, 1; 367.

*Peropteryx macrotis macrotis,* G. M. Allen, 1935, Jour. Mamm., 16:227.

*Specimens*: ALAJUELA: 4 km NE La Palmira, Finca Las Vegas, 400 m, 1 ♀; 8.2 miles W bridge at Atenas on road to San Matéo, 671 m, 1 ♀. LIMON: 1 mile NW Limón, Les Cuevas, sea level, 1 ♂, 2 ♀♀. PUNTARENAS: Boca de Barranca, sea level, 1 ♀; 35 miles SE San Isidro del General along Interamerican Highway, at bridge over Río Ceibo, 320 m, 1 ♀. SAN JOSE: Río Cañas, Las Cuevas, 200 m, 2 ♂♂.

*Measurements*: Averages and ranges: forearm (3 males, 6 females, respectively), 42.6 (41.9-43.0), 45.4 (43.8-46.9); (cranial, males and females together) greatest length of skull (7 specimens), 14.9 (14.5-15.3); length of

maxillary toothrow, C-$M^3$ (9), 5.8 (5.5-6.0); postorbital constriction (9), 2.9 (2.7-3.2); zygomatic breadth (9), 8.5 (8.3-8.8).

*Remarks*: These nine specimens mark the first records of *P. macrotis* for Costa Rica, although the species is known from southern Mexico to and throughout tropical South America (Hall and Kelson, 1959; Sanborn, 1937). The Costa Rican specimens are all from lower elevations and represent both Pacific and Caribbean slopes. They were shot at night over roads in areas where trees (but not necessarily forest) occurred, or were taken from diurnal roosts in caves (Limón, Río Cañas, Finca Las Vegas). Although *P. macrotis* was collected in association with *P. kappleri* in all three of the roosts, the two species were never taken together while feeding over the roads at night. The roosting *Peropteryx* were found in rather open situations at or very near the mouths of the caves.

### **Centronycteris maximiliani centralis** Thomas

*Centronycteris centralis* Thomas, 1912, Ann. Mag. Nat. Hist., ser. 8, 10: 638.
*Centronycteris maximiliani centralis*, Sanborn, 1937, Zool. Ser. Field Mus. Nat. Hist., 20: 337.

*Specimens*: PUNTARENAS: Rincón de Osa, Osa Productos Forestales, Camp Seattle, 35 m, 2 ♀♀, and near headquarters area, 10 m, 1 ♀.

*Measurements*: Forearm (3 females), 42.7, 44.2, 44.4; (cranial, third female) greatest length of skull, 14.4; condylobasal length, 13.2; length of maxillary toothrow, C-$M^3$, 5.9; postorbital constriction, 3.0; zygomatic breadth, 9.1; breadth across $M^3$-$M^3$, 6.1.

*Remarks*: This species is known from relatively few localities from southern Mexico to southern Brazil (Hall and Kelson, 1959; Handley, 1966; Sanborn, 1937) and was first recorded from Costa Rica, without definite locality, by Allen and Barbour (1923). The same specimen was later listed by Sanborn (1937) as coming from Viragua, Prov. Alajuela, and then by Goodwin (1946) from Vijagua, Prov. Alajuela. Sanborn's spelling was in error: the label on the specimen (MCZ 7092) reads "Vijagua, Costa Rica," Vijagua being an alternative spelling for Bijagua, or La Bijagua, a small town on the Caribbean slope of Volcán Miravalles, Prov. Alajuela (some 320 km NW of Rincón de Osa).

The rarity of specimens of *C. maximiliani*, in the light of our limited experience with this bat, suggests that it requires relatively heavy forest (possibly virgin stands) in which to live. The very slow and highly maneuverable, floppy flight of this species makes it well adapted to hunting insects among trees and along natural (and now man-made) pathways and clearings. The three specimens reported here were all collected in just such situations.

### **Balantiopteryx plicata plicata** Peters

*Balantiopteryx plicata* Peters, 1867, Monatsb. preuss. Akad. Wiss., Berlin, p. 476.

*B* [*alantiopteryx*] *p* [*licata*] *plicata,* Burt, 1948, Occ. Pap. Mus. Zool., Univ. Mich., No. 515, p. 2.

*Specimens*: GUANACASTE: Playas del Coco, sea level, 16 ♂♂, 17 ♀♀; Mico de Matapalo, 50 m, 13 ♂♂, 1 ♀.

*Measurements*: Averages and ranges: forearm (22 males, 10 females, respectively), 40.0 (39.0- 42.3), 42.0 (40.2- 43.2); (cranial, 2 males, 2 females together) greatest length of skull, 14.4 (14.2-14.6); condylobasal length, 13.0 (12.9-13.1); length of maxillary toothrow, C-$M^3$, 5.4 (5.4); interorbital breadth, 5.5 (5.4-5.5); postorbital constriction, 3.1 (2.9-3.3); zygomatic breadth, 9.1 (8.9-9.2); breadth of braincase, (3 specimens), 6.9 (6.9-7.0); mastoid breadth, 8.1 (7.9-8.1); alveolar breadth across upper canines, 3.6 (3.5-3.7); breadth across $M^3$-$M^3$, 6.6 (6.5-6.6).

*Remarks*: Since the description of *B. plicata* in 1867, based on one specimen from "Puntarenas in Costa Rica," this bat has been collected from a number of localities, and often in rather large numbers, from tropical Mexico, Guatemala and El Salvador (Hall and Kelson, 1959; Felten, 1955; Burt and Stirton, 1961), but only recently has it been reported from localities further to the south. Jones (1964) includes a single specimen from each of two localities in Nicaragua, and this paper records the first specimens to be taken in Costa Rica since the type description. Hall and Kelson (1959) assume Peters' type locality to be Puntarenas, Prov. Puntarenas, but since the place name is used to refer to both the town and the province and Peters did not specify more than "Puntarenas," the exact type locality must remain open to question. Because most (if not all) of the known specimens of this bat apparently come from localities in the relatively drier portions of Middle America, usually on the Pacific side of the cordillera (all localities in Central America), it is *most likely,* on ecogeographic grounds, that the type of *B. plicata* came from the lowland Tropical Dry Forest region in the small portion of Puntarenas Province north and northwest of Punta Leona (some 10 km south of the Río Grande de Tárcoles), if not actually from the town of Puntarenas itself.

Both series of *Balantiopteryx* recorded here came from colonies in diurnal roosts. The specimens from Playas del Coco were roosting in a series of fissures in the face of a sea cliff which was accessible only at low tide; those from Mico de Matapalo were hanging in the shadow of a huge rafter near the mouth of a short, partially collapsed, abandoned manganese mine. The bats taken from the latter colony were all adults (January 26, 1963), while the former series included 18 adults, 14 subadults and one large juvenile (August 27, 1962).

### **Diclidurus virgo** Thomas

*Diclidurus virgo* Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, 11: 337.

*Specimen*: PUNTARENAS: 2.7 miles NW Villa Neilly along Interamerican Highway, at bridge over Río Nuevo, *55 m,* 1 ♀.

*Measurements*: Forearm, 65.0; greatest length of skull (to front of canines), 18.4; condylobasal length, 17.6; length of maxillary toothrow, C-$M^3$,

7.9; interorbital breadth, 8.7; postorbital constriction, 5.6; zygomatic breadth, 12.1; breadth of braincase, 9.2; mastoid breadth, 10.2; alveolar breadth across upper canines, 4.4; breadth across $M^3$-$M^3$, 8.4.

*Remarks*: This specimen is apparently the first record from the Costa Rican lowlands for this species, which is known by relatively few records from Oaxaca, Mexico, to western Panama (Hall and Kelson, 1959; Handley, 1966). It has been reported previously from Costa Rica from three localities, all of which are on the Meseta Central (central plateau)—Escazú (type locality), San José and La Palma (all Prov. San José)—at elevations ranging approximately from 1100 to 1500 m (with some leeway, depending on the exact localities represented by the locality names). The Río Nuevo individual was shot at night as it hawked insects over the road, flying relatively high and apparently straight courses, out of the range of the lights of the field truck, and uttering a unique musical twittering not heard in other Costa Rican bats. On the night this bat was collected (September 9, 1963), we had parked the truck by the road and a phenomenal number of moths were swarming in the headlights. Numerous bats were dodging in and out of the headlight beams, snapping up the moths and other insects, and within about an hour (starting at dusk or approximately 6:00 PM local time) we collected a number of *Saccopteryx bilineata* and *Pteronotus suapurensis* as they chased insects in our lights, as well as the *Diclidurus,* which was making passes above the truck. The peculiar musical call of the white bat was heard above us in the dark during most of the time until the specimen was shot, after which the sound was noticeably absent from the night air.

White bats, which were almost certainly *Diclidurus* and not the smaller and undoubtedly less conspicuous *Ectophylla alba,* were mentioned by local people at Boca de Barranca, Prov. Puntarenas (sea level, Pacific lowlands) and Finca La Lola, Prov. Limón (50 m, Caribbean lowlands). In both places they were said to have been seen hanging from beneath the leaves of coco palms during the day. One was shot by one of the men working at Pension Chanita, Boca de Barranca, in 1959 (and thrown away).

### **Cyttarops alecto** Thomas

*Cyttarops alecto* Thomas, 1913, Ann. Mag. Nat. Hist., ser. 8, 11: 134.

*Specimens*: HEREDIA: Puerto Viejo de Sarapiquí, 100 m, 3 ♂♂, 5 ♀♀.

*Measurements*: Forearm (male, 3 females, respectively), 45.8, 47.1, 46.7, 46.6; (cranial, same male, first two females) greatest length of skull, 13.6, ——, 14.3; condylobasal length, 12.6, ——, 13.1; length of maxillary toothrow, C-$M^3$, 5.4, 5.6, 5.5; interorbital breadth, 5.1, ——, ——; postorbital constriction, 4.2, 3.7, 3.9; zygomatic breadth, 8.7, ——, ——; breadth of braincase, 7.1, 7.1, 7.1; mastoid breadth, 7.7, ——, 7.6; alveolar breadth across upper canines, 3.0, ——, ——; breadth across $M^3$-$M^3$, 6.3, ——, ——; length of mandibular toothrow, C-$M^3$, 6.0, 6.0, 5.9.

*Remarks*: This rare bat was represented only by the type specimen from

Para, Brazil, and a second specimen from British Guiana (also used in the original description) until 1964, when three specimens were recorded from Los Diamantes, Prov. Limón (300 m), with a fuller description of its characters (Starrett and De la Torre, 1964). The eight specimens reported here were collected at a town some 35 km northwest of Los Diamantes and also on the Caribbean lowlands, and constitute the fourth locality record for this monotypic genus. These bats were shot during the day as they hung, in small groups, from beneath the fronds of coco palms in the town of Puerto Viejo, on three successive days (September 15-17, 1964). The series includes one adult male, four adult females, two subadult males and one subadult female (LACM 26614-26617, 26625-26627, 26633). The specimens are in a better state of preservation than those from Los Diamantes (LACM 14572-14574), which were collected from a coco palm by some workers and preserved in local alcohol. The new specimens show color variation in that some of the adults have a somewhat paler gray area in the region of the shoulders and dorsal portion of the base of the neck. In other respects they agree with those from Los Diamantes and with the type description.

### **Noctilio leporinus mexicanus** Goldman

*Noctilio leporinus mexicanus* Goldman, 1915, Proc. Biol. Soc. Wash., 28: 136.

*Specimens*: LIMON: Tortuguero, sea level, 1 ♀ (UF 4647). PUNTARENAS: Boca de Barranca, sea level, 1 ♂, 1 ♀; Río Coronado, 20 km NW Puerto Cortés, sea level, 1 ♀; Dominical, sea level, 1 ♀.

*Measurements*: Forearm (1 male, 3 females, respectively), 82.9, 85.0, 82.0, 83.9; (cranial, male and first female) greatest length of skull, 27.5, 26.1; condylobasal length, 23.9, 23.3; length of maxillary toothrow, C-$M^3$, 10.4, 10.0; postorbital constriction, 7.2, 7.0; zygomatic breadth, 19.2, 18.2; mastoid breadth, 17.8, 16.4; breadth across $M^3$-$M^3$, 12.5, 12.3.

*Remarks*: Although this fish-eating bat ranges throughout most of the Neotropics (Cabrera, 1957; Hall and Kelson, 1959) and has been known from Panama since 1923 (Allen and Barbour, 1923), it was first recorded from Nicaragua in 1964 (Davis *et al.*, 1964) and from Costa Rica in 1966 (Carter *et al.*, 1966). The additional specimens here reported were caught in mist nets set either across or parallel to streams, rivers or creeks near the ocean (with estuarine tidal influence at Boca de Barranca). At Hacienda Bonilla, near Boca de Barranca, we watched fish-eating bats, along with *Rhynchonycteris,* coursing over a long rain "puddle" (roughly five by 30 yards in extent) containing minnow-sized fish. *Saccopteryx bilineata, Molossus* sp. and seven species of phyllostomatids were taken in various combinations in the same nets with *N. leporinus* at the three localities.

### **Pteronotus davyi** Gray

*Pteronotus davyi* Gray, 1838, Mag. Zool. Bot., 2: 500.

*Chilonycteris gymnotus* Wagner, 1843, Arch. Naturgeschichte, 9 (Bd. 1): 367.

*Chilonycteris davyi fulvus* Thomas, 1892, Ann. Mag. Nat. Hist., ser. 6, 10: 410.
*Dermonotus davyi,* Miller, 1902, Proc. Biol. Soc. Wash., 15: 155.
*Pteronotus davyi davyi,* Miller, 1912, Bull. U.S. Nat. Mus., 79: 33.
*Pteronotus davyi fulvus,* Miller, 1912, Bull. U.S. Nat. Mus., 79: 33.

*Specimens*: ALAJUELA: 4.6 miles (1067 m) and 8.4 miles (671 m) W bridge at Atenas on road to San Matéo, 1 ♂, 2 ♀♀. GUANACASTE: Playas del Coco, sea level, 1 ♀; 5 miles N Liberia along Interamerican Highway, 150 m, 1 ♀.

*Measurements*: Averages and ranges (4 females): forearm, 45.7 (44.7-47.6); greatest length of skull, 16.1 (15.8-16.5); condylobasal length, 14.9 (14.7-15.2); length of maxillary toothrow, C-$M^3$, 6.7 (6.5-6.8); postorbital constriction, 3.7 (3.5-3.8); zygomatic breadth (3 females), 8.9 (8.9-9.0); breadth of braincase, 7.9 (7.7-8.0); mastoid breadth, 8.5 (8.0-8.8); alveolar breadth across upper canines, 4.8 (4.8-4.9); breadth across $M^3$-$M^3$, 6.0 (6.0); length of mandibular toothrow, C-$M_3$, 7.1 (7.0-7.1); length of mandible, 12.0 (11.8-12.1).

*Remarks*: Previous to the collection of the specimens reported here, there has been a gap, which extended from El Salvador (Hall and Kelson, 1959) to Venezuela (Cabrera, 1957), in the distribution of this tropical American species. The northern and Antillean-southern populations were distinguished as subspecies when Thomas (1892) described *P. d. fulvus* from Mexico. Apparently, however, the species essentially is distributed continuously. A comparison of measurements of the specimens from Costa Rica with those of *P. d. fulvus* (including the type) from Mexico (Goodwin, 1946; LACM specimens) and El Salvador (Burt and Stirton, 1961; Felten, 1956a) and *P. d. davyi* from Trinidad (Dobson, 1878; Goodwin, 1946; Goodwin and Greenhall, 1961) indicates that, although some clinal variation may exist, these forms do not warrant taxonomic distinction (as has already been suggested by J. A. Allen, 1894). The status of the *P. davyi* mentioned by Goodwin (1946), from the Island of Dominica, may be open to question.

The specimen of *P. davyi* from Playas del Coco was caught, along with seven species of phyllostomatids and *Desmodus,* in a mist net set over a stream. The other four were all shot over roads at night, the three from the road to San Matéo while they were flying low hunting courses along the roadside vegetation. Also shot with the latter were *Peropteryx macrotis* and *Eptesicus furinalis gaumeri.*

### **Pteronotus suapurensis suapurensis** (J. A. Allen)

*Dermonotus suapurensis* J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., 20: 229.
*Pteronotus suapurensis,* J. A. Allen, 1911, Bull. Amer. Mus. Nat. Hist., 30: 265.
*Pteronotus davyi suapurensis,* G. M. Allen, 1935, Jour. Mamm., 16: 227.
*Pteronotus suapurensis centralis* Goodwin, 1942, Jour. Mamm., 23: 88.

*Pteronotus suapurensis suapurensis,* Davis, Carter and Pine, 1964, Jour. Mamm., 45: 377.

*Specimens*: PUNTARENAS: 35 miles SE San Isidro del General along Interamerican Highway, near bridge over Río Ceibo, 320 m, 1 ♂; 2.7 miles NW Villa Neilly, at bridge over Río Nuevo, *55 m,* 3 ♂♂, 3 ♀♀.

*Measurements*: Forearm (averages and ranges, 4 males, 3 females, respectively), 52.7 (51.9-53.6), 50.9 (50.5-52.3); (cranial, first two males, second and third females) greatest length of skull, 18.1, 17.7, 17.9, 16.9; condylobasal length, 16.9, 16.7, 16.7, 16.3; length of maxillary toothrow, C-$M^3$, 7.8, 7.5, 7.5, 7.2; postorbital constriction, 4.4, 4.3, 4.1, 4.4; zygomatic breadth, 10.6, 10.2, 10.1, ——; breadth of braincase, 9.0, 8.5, 8.6, 8.5; mastoid breadth, 9.4, 9.4, ——, 9.8; alveolar breadth across upper canines, 6.0, 5.7, 5.4, 5.8; breadth across $M^3$-$M^3$, 7.3, 7.0, 6.9, 7.0; length of mandibular toothrow, C-$M_3$, 8.3, 7.9, 7.9, 7.7; length of mandible, 14.1, 13.6, 13.5, 13.1.

*Remarks*: This species, which is known from a limited number of localities from Veracruz, Mexico (Davis *et al.,* 1964), through Central America into northern South America (Cabrera, 1957; Hall and Kelson, 1959), has been recorded previously from Costa Rica from Boruca (562 m), Prov. Puntarenas (Carnegie Museum 1613, Sanborn, 1932). The nearest neighboring records are from one locality in Nicaragua (Goodwin, 1942) and six in Panama (Handley, 1966). Our specimens come from two localities which are both within 60 km of Boruca: all were shot over roads at night, the specimen from Río Ceibo with *Peropteryx macrotis* and those from Río Nuevo with *Saccopteryx bilineata* and *Diclidurus virgo.*

### **Chilonycteris psilotis** Dobson

*Chilonycteris psilotis* Dobson, 1878, Cat. Chiroptera British Mus., p. 451.

*Chilonycteris torrei continentis* Sanborn, 1938, Occ. Pap. Mus. Zool., Univ. Mich., No. 373, p. 1.

*Specimens*: GUANACASTE: 4.4 miles S Liberia, 125 m, 1 ♀. PUNTARENAS: Rincón de Osa, Osa Productos Forestales, Camp Seattle, 35 m, 1 ♀.

*Measurements*: Forearm 45.4, 47.0; greatest length of skull, ——, 15.6; condylobasal length, ——, 14.2; length of maxillary toothrow, C-$M^3$, 6.2, 6.2; postorbital constriction, 3.6, 3.5; zygomatic breadth, 8.5, 8.5; breadth of braincase, 7.2, 7.4; mastoid breadth, 8.3, 8.7; alveolar breadth across upper canines, 4.4, 4.4; breadth across $M^3$-$M^3$, 5.6, 5.8.

*Remarks*: This species, which apparently occurs from tropical Mexico at least to Venezuela (De la Torre, 1955), has been recorded previously in Central America south of El Salvador (Burt and Stirton, 1961) only from localities in Panama (Handley, 1966). Goodwin and Greenhall (1961) consider this small *Chilonycteris* a subspecies of *C. personata* Wagner. However, at this point, without the opportunity to make a fuller study of the necessary comparative material, we are following De la Torre (1955) in considering

*C. psilotis* Dobson (type locality: Oaxaca, Mexico) specifically distinct from *C. personata* Wagner (type locality: Matto Grosso, Brazil) and assigning the Costa Rican specimens to the former.

We prefer to retain the generic distinction between the "naked-backed" species *(Pteronotus)* and those with the wing membranes attached farther down on the sides of the body *(Chilonycteris)*. The distinction is clear and definitive, in spite of the fact that there is some variation in this character among the species of *Chilonycteris*, as pointed out by Burt and Stirton (1961) in their discussion which argued in favor of considering all the species of the two genera as congeneric, under the name *Pteronotus*.

Both LACM specimens were shot over the road at night, the one from Rincón de Osa while it was hunting relatively low over the ground and vegetation next to a small swamp.

### **Micronycteris schmidtorum** Sanborn

*Micronycteris schmidtorum* Sanborn, 1935, Zool. Ser., Field Mus. Nat. Hist., 20: 81.

*Specimens*: GUANACASTE: 3 km S Playas del Coco, *70 m*, 1 ♂, 5 ♀♀; 9 km N Liberia along Interamerican Highway and 4 km E Interamerican Highway, *150 m*, 1 ♂.

*Measurements*: Forearm (2 males, average and range of 5 females, respectively), 33.1, 34.0, 35.1 (34.6-35.9); (cranial, 2 males, third and fifth females) greatest length of skull, 20.4, 19.8, 19.8, 20.0; condylobasal length, 17.1, 17.0, 17.7, 17.5; length of maxillary toothrow, C-$M^3$, 7.7, 7.8, 7.6, 7.8; postorbital constriction, 4.2, 4.3, 4.3, 4.4; zygomatic breadth, 9.3, 9.5, 9.1, 9.4; breadth of braincase, 8.2, 7.9, 7.9, 8.1; mastoid breadth, 9.2, 9.0, 9.0, 8.8; alveolar breadth across upper canines, 3.3, 3.3, 3.4, 3.2; breadth across $M^3$-$M^3$, 6.4, 6.1, 6.2, 6.1; length of mandibular toothrow, C-$M_3$, 8.2, 8.4, 8.3, 8.3; greatest length of lower premolar series, 3.0, 3.0, 3.1, 3.0.

*Remarks*: These specimens mark the first Costa Rican records for this bat, which was previously known from four localities from Yucatan, Mexico, to southeastern Nicaragua (Hall and Kelson, 1959; Davis *et al.*, 1964), and one locality in Panama (Handley, 1966). The bats from near Playas del Coco were all taken from one hollow tree (on two successive days); that from near Liberia was captured, along with five other genera of phyllostomatids, in a mist net set across a small stream.

### **Macrophyllum macrophyllum** (Schinz)

*Phyllost* [*oma*] *macrophyllum* Schinz, 1821, Das Thierreich . . . . ., 1: 163.
*Macrophyllum macrophyllum*, Nelson, 1912, Proc. Biol. Soc. Wash., 25: 93.

*Specimens*: GUANACASTE: Río Colorado, 9 km N Liberia along Interamerican Highway and 4 km E Interamerican Highway, *150 m*, 5 ♂♂ (1 imm.). LIMON: Finca La Lola, Río Madre de Dios, 50 m, 1 ♀.

*Measurements*: Female, Río Madre de Dios (LACM 15147), male, Río Colorado (LACM 23365), respectively: forearm 35.3, 34.4; greatest length of skull, 16.9, 17.2; condylobasal length, 13.8, 14.2; length of maxillary toothrow, C-$M^3$, 5.3, 5.6; postorbital constriction, 3.3, 3.2; zygomatic breadth, 9.4, 9.6; mastoid breadth, 8.7, 9.0; alveolar breadth across upper canines, 3.5, 3.4; breadth across $M^3$-$M^3$, 6.4, 6.3; length of mandibular toothrow, 5.9, 6.0.

*Remarks*: These specimens appear to be the first records of *Macrophyllum* from Costa Rica. Previous published records for Central America, including localities in Nicaragua and Panama, are discussed by Davis *et al.* (1964), Jones (1964), and Handley (1966).

The female from La Lola was caught early in the evening in a mist net set across the Río Madre de Dios. The five males from the Río Colorado were taken from a diurnal roost in an irrigation tunnel, along with numerous *Carollia* sp. and *Chilonycteris parnellii.*

### **Trachops cirrhosus** (Spix)

*Vampyrus cirrhosus* Spix, 1823, Simiarum et vespertilionum Braziliensum. . . ., p. 64.

*Trachops fuliginosus* Gray, 1865, Proc. Zool. Soc. Lond., p. 14.

*Specimens*: PUNTARENAS: Boca de Barranca, 5 m, 9 ♂♂, 8 ♀♀; Dominical, 3 m, 5 ♂♂, 5 ♀♀; 5 km N Villa Neilly on Interamerican Highway, 150 m, 1 ♂; Monteverde, Río Guacimal, 1380 m, 1 ♂.

*Measurements*: Two females, averages and ranges for 4 males, respectively: forearm, 59.7, 61.1, 59.1 (57.3-61.7); greatest length of skull, 28.1, 27.7, 28.5 (28.3-29.1); condylobasal length, ——, 24.3, 24.7 (24.6-24.9); length of maxillary toothrow, C-$M^3$, 9.9, 9.8, 10.1 (10.1-10.2); postorbital constriction, 5.3, 5.2, 5.4 (5.1-5.3); zygomatic breadth, 13.5, 13.6, 13.7 (13.6-13.9); mastoid breadth, 13.0, 13.2, 13.3 (13.1-13.4); alveolar breadth across upper canines, 11.1, 11.1, 11.4 (11.1-11.9); breadth across $M^3$-$M^3$, 9.5, 9.7, 9.8 (9.7-9.9); length of mandibular toothrow, 10.8, 10.8, 11.0 (10.8-11.2).

*Remarks*: This species has been reported previously from only one locality in Costa Rica: Río Tenorio, 3 miles S and 10 miles W Las Cañas, 3 m, Prov. Guanacaste (Davis and Carter, 1962). The next closest localities are in Honduras (Goodwin, 1942) and Panama (Handley, 1966). Felten (1956b) considers *Trachops coffini* Goldman to be a subspecies of *T. cirrhosus* and uses the name *T. cirrhosus coffini* for specimens from El Salvador, as do also Burt and Stirton (1961). Handley (1966) lists the *Trachops* from Panama as *T. c. cirrhosus.* Examination of further comparative material will be necessary in order to clarify the subspecies question in this genus and determine which name should be used for specimens from Costa Rica.

The specimens from Boca de Barranca were taken during the day from an abandoned railroad tunnel, on four different dates from July, 1962, to late June, 1963. Those from Dominical and near Villa Neilly were caught in

culverts in daytime. The Monteverde specimen was captured in a mist net set across a narrow stream gorge.

### **Chrotopterus auritus** Peters

*Vampyrus auritus* Peters, 1856, Abhandl. preuss. Akad. Wiss., Berlin, p. 305.
*Chrotopterus auritus,* Peters, 1865, Monatsb. preuss. Akad. Wiss., Berlin, p. 505.

*Specimens*: LIMON: Finca La Lola, 50 m, 7 ♂♂ (1 imm.), 1 ♀.

*Measurements*: Female, 3 males, respectively: forearm, 83.0, 79.3, 79.7, 79.8; greatest length of skull, 38.5, 36.9, 37.4, 37.9; condylobasal length, 32.9, 31.4, 32.0, 32.4; length of maxillary toothrow, C-$M^3$, 13.9, 13.5, 13.5, 13.8; postorbital constriction, 15.9, 15.7, 16.1, 16.0; zygomatic breadth, 19.5, 18.4, 19.3, 18.9; mastoid breadth, 17.1, 16.6, 16.9, 16.7; alveolar breadth across upper canines, 17.8, 17.2, 17.8, 17.4; breadth across $M^3$-$M^3$, 12.3, 11.5, 12.2, 12.0; length of mandibular toothrow, 15.9, 15.1, 15.6, 15.5.

*Remarks*: These specimens represent the first Costa Rican records for this species. *Chrotopterus* has been reported previously from Mexico (Hall and Kelson, 1959; Davis *et al.,* 1964), El Salvador (Burt and Stirton, 1961), Guatemala (Carter *et al.,* 1966), Panama (Handley, 1966), and South America (Cabrera, 1957).

The first seven specimens were taken from a diurnal roost in a large hollow tree (July 30, 1961). When the tree was revisited in September, 1962, a large colony of vampires (*Desmodus rotundus*) were occupying the tree and only one male *Chrotopterus* was present.

### **Vampyrodes major** G. M. Allen

*Vampyrodes major* G. M. Allen, 1908, Bull. Mus. Comp. Zool., 52: 38.
*Vampyrodes ornatus* Thomas, 1924, Ann. Mag. Nat. Hist., ser. 9, 13: 532.
*Vampyrodes caraccioloi ornatus,* Cabrera, 1957, Rev. Mus. Argent. Cien. Nat. "Bernardino Rivadavia," Cien. Zool., 4: 82.
*Vampyrodes carracioloi major,* Carter, Pine and Davis, 1966, Southwest. Nat., 11: 494.
*Vampyrodes caraccioloi major,* Handley, 1966, p. 766, *in* Wenzel and Tipton, Ectoparasites of Panama.

*Specimens*: HEREDIA: Puerto Viejo de Sarapiquí, 100 m, 1 ♂ (KU 88153). LIMON: Finca La Lola, 50 m, 1 ♀; Los Diamantes, 100 m, 3 ♂♂, 7 ♀♀. PUNTARENAS: Rincón de Osa, Osa Productos Forestales, near Río Rincón, 5 m, 1 ♀.

*Measurements*: (Averages and ranges): forearm (3 males, 9 females), 53.1 (52.2-54.4); (cranial, 3 males, 2 females) greatest length of skull, 27.9 (27.4-28.4); condylobasal length, 24.5 (24.4-24.7); length of maxillary toothrow, C-$M^2$, 9.9 (9.8-10.1); postorbital constriction, 6.8 (6.6-7.0); zygomatic breadth, 17.2 (16.7-17.8); breadth of braincase, 12.0 (11.7-12.2);

mastoid breadth, 13.9 (13.7-14.3); alveolar breadth across upper canines, 6.9 (6.8-7.3); breadth across $M^2$-$M^2$, 12.4 (12.0-12.6).

*Remarks*: *Vampyrodes major* has been recorded previously in Costa Rica only from Cerro Santa Maria, Prov. Alajuela (Goldman, 1920). This bat is apparently not uncommon at lower elevations on both coasts, although it seems to prefer the wetter portions of the country. Our specimens were all captured in mist nets.

From a comparison of specimens, published data and the original descriptions of *Vampyrodes major, V. ornatus* Thomas, and *V. caracciolae* Thomas, it seems that there is no reason for retaining *V. ornatus* as a species distinct from *V. major* nor, in fact, for even distinguishing the two subspecifically (in agreement with Handley, 1966). The measurements of *V. ornatus,* as well as its salient characters, fit in with those of *V. major* (including the type and LACM series of the latter from Costa Rica and Mexico) and there seems to be no break in these features anywhere in the ranges of localities represented by the two names. *V. caracciolae,* on the other hand, appears to be a distinct, smaller, and less brightly colored species which deserves specific status (contrary to the opinions of Cabrera, 1957, Goodwin and Greenhall, 1961, and Handley, 1966). Two obvious dental characters separate *V. major* from *V. caracciolae*: the former has distinctly bifid and rounded outer upper incisors while in *V. caracciolae* these teeth are entire with a more flattened profile (a character illustrated by Thomas, 1889, and by Goodwin and Greenhall, 1961, but otherwise apparently overlooked); the $M_1$ of *V. major* has a distinct cusplet arising from the anterolingual portion of the cingulum, whereas this structure is absent in *V. caracciolae.* The small size of the male *Vampyrodes* from Utinga, Pará, Brazil, mentioned by Thomas (1920), suggests that it also belongs to the latter species rather than to *V. major.* Since the specimen from Pará apparently was returned to Brazil, Thomas' inclusion of it in *V. caracciolae* will have to remain as the standing opinion on this matter until the dental characters can be checked. *V. major* is currently known from Peru (San Lorenzo, Depto. Loreta: type locality of *V. ornatus*) and most of the countries in Middle American from Panama to Mexico (summarized by Davis *et al.,* 1964, and Handley, 1966), and has a distribution quite separate from that of *V. caracciolae.* Further collecting in the intermediate areas in South America may bring the two ranges closer together.

### **Ectophylla alba** H. Allen

*Ectophylla alba* H. Allen, 1892, Proc. U.S. Nat. Mus., 15: 441.

*Specimens*: CARTAGO: Turrialba, Instituto Interamericano de Ciencias Agrícolas, 602 m, 1 ♂ (ISU 230), 1 (?) (IICA). HEREDIA: Finca "La Selva," near Puerto Viejo de Sarapiquí, 100 m, 2 ♀♀.

*Measurements*: Forearm (male, 2 females), 28.1 (dry), 28.6, 29.5; (cranial, male) greatest length of skull, 17.0; condylobasal length, 15.8; length of maxillary toothrow, C-$M^2$, 6.1; zygomatic breadth, 10.6; breadth of brain-

case, 6.2; mastoid breadth, 8.8; alveolar breadth across upper canines, 4.3; breadth across $M^2$-$M^2$, 7.6; length of mandibular toothrow, C-$M_2$, 6.6.

*Remarks*: The Turrialba specimens represent the third locality for the little white bat in Costa Rica, extending its range some 65 km to the South-southeast from Finca "La Selva" from which three specimens have previously been reported (Casebeer *et al.*, 1963: see also for a summary and discussion of earlier records). This species is known only from the Caribbean lowlands of Nicaragua, Costa Rica and Panama (Handley, 1966), ranging from an unknown elevation (undoubtedly well below 300 m) at the type locality on the Río Coco (Río Segovia), Nicaragua, to approximately 602 m at Turrialba and 732 m in Panama (Handley, 1966). All specimens of this bat were caught in mist nets.

### **Mesophylla macconnelli** Thomas

*Mesophylla macconnelli* Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, 8: 143.
*Ectophylla macconnelli,* Laurie, 1955, Ann. Mag. Nat. Hist., ser. 12, 8: 269.
*E*[*ctophylla*] *m*[*acconnelli*] *macconnelli,* Goodwin and Greenhall, 1962, Amer. Mus. Nov., no. 2080, p. 3.
*Ectophylla macconnelli flavescens* Goodwin and Greenhall, 1962, Amer. Mus. Nov., no. 2080, p. 2.
*Ectophylla macconnelli,* Handley, 1966, p. 768, *in* Wenzel and Tipton, Ectoparasites of Panama.

*Specimens*: CARTAGO: Moravia de Chirripó, 1116 m, 1 ♀ (UMMZ 111724).

*Measurements*: Forearm, 33.0; greatest length of skull, 18.5; condylobasal length, 16.7; length of maxillary toothrow, C-$M^2$, 6.3; postorbital constriction, 4.5; zygomatic breadth, 10.4; breadth of braincase, 8.1; mastoid breadth, 9.2; alveolar breadth across upper canines, 4.4; breadth across $M^2$-$M^2$, 7.7; length of mandibular toothrow, 7.1.

*Remarks*: This bat has been reported previously from several localities in Panama, widespread localities in tropical South America, and from Trinidad (Handley, 1966; Cabrera, 1957; Goodwin and Greenhall, 1962). The specimen from Costa Rica is much grayer in color than LACM specimens of *M. macconnelli* from Peru and Brazil, and is apparently even grayer than *M. m. flavescens* (Goodwin and Greenhall) from Trinidad. Its measurements are generally larger than those of *M. m. macconnelli* listed by Goodwin and Greenhall (1962) and approach those of *M. m. flavescens.* Handley (1966) considers the species to be monotypic, on the basis of variability in Panamanian specimens, and we follow Handley's judgment in this matter at this time.

We disagree with Laurie (1955) and Goodwin and Greenhall (1962), and consider *Mesophylla* Thomas to be a genus distinct from *Ectophylla* H. Allen in several prominent cranial, as well as dental, features. The genera *Ectophylla, Mesophylla* and *Vampyressa* Thomas form a well-defined group

within the Stenoderminae, sharing cranial, dental and external characters, and showing varying degrees of modification of a similar dentitional pattern. The skull of *Vampyressa pusilla thyone* shows more similarity to that of *Mesophylla* than does the skull of *Ectophylla,* and exhibits dental features seen in both the other genera. *Ectophylla,* with its shortened rostrum, raised nasals, and exaggerated circular and flattened last lower molar ($M_2$), appears to be the most highly modified of the three genera, and we see no justification for making it congeneric with *Mesophylla.*

### **Natalus stramineus mexicanus** Miller

*Natalus mexicanus* Miller, Proc. Acad. Nat. Sci. Philadelphia, 54: 399.

*Natalus mexicanus mexicanus,* Dalquest and Hall, 1949, Proc. Biol. Soc. Wash., 62: 153.

*Natalus mexicanus saturatus* Dalquest and Hall, 1949, Proc. Biol. Soc. Wash., 62: 153.

*Natalus stramineus saturatus,* Goodwin, 1959, Amer. Mus. Nov., no. 1977, p. 7.

*Natalus stramineus mexicanus,* Handley, 1966, p. 770, *in* Wenzel and Tipton, Ectoparasites of Panama.

*Specimens*: GUANACASTE: Curiol de Santa Rosa, 25 m, 3 ♂♂.

*Measurements*: Forearm, 36.9, 36.4, 36.4; (cranial, second specimen) greatest length of skull, 16.4; condylobasal length, 15.0; length of maxillary toothrow, C-$M^3$, 6.9; postorbital constriction, 3.1; zygomatic breadth, 8.4; breadth of braincase, 7.8; alveolar breadth across upper canines, 3.6; breadth across $M^3$-$M^3$, 5.5.

*Remarks*: These specimens mark the first records for this genus in Costa Rica. The species (following Cabrera, 1957, and Goodwin, 1959) ranges from tropical Mexico into eastern South America (to Brazil), but until now it has not been recorded from any country between El Salvador and Panama (Hall and Kelson, 1959; Handley, 1966).

The *Natalus* from Costa Rica were caught during the day, in a mist net stretched across the entrance to an abandoned tungsten mine, as they attempted to escape capture in the mine tunnel. Also taken in the same tunnel were *Saccopteryx bilineata* (near the entrance to a small side opening), *Chilonycteris parnellii, Carollia subrufa, Glossophaga soricina,* and *Desmodus.*

### **Myotis simus riparius** Handley

*Myotis simus riparius* Handley, 1960, Proc. U.S. Nat. Mus., 112: 466.

*Specimen*: CARTAGO: 4 km SW Moravia de Chirripó, 1200 m, 1 ♀ (KU 88207).

*Measurements*: Forearm, 40.4; greatest length of skull, 14.8; condylobasal length, 13.8; length of maxillary toothrow, C-$M^3$, 5.7; postorbital constriction, 3.5; zygomatic breadth, 8.9; breadth of braincase, 6.7; alveolar breadth across upper canines, 3.7; breadth across $M^3$-$M^3$, 5.8.

*Remarks*: This specimen marks the first record of *Myotis simus* for Costa Rica and extends the range of the subspecies into Central America from eastern Panama (Handley, 1966). This same specimen was recently reported as *Myotis albescens* by Nelson (1965).

### **Myotis chiloensis** (Waterhouse)

*Vespertilio chiloënsis* Waterhouse, 1838, Zool. Voy. Beagle, p. 5, pl. 3.
*Myotis chiloënsis,* Cabrera, 1903, Rev. Chilena Hist. Nat., 7: 295.

*Specimen*: SAN JOSE: Cerro de la Muerte, on Interamerican Highway, 4.3 miles S restaurant "La Georgina," 2590 m, 1 ♂ (LACM 25445).

*Measurements*: Forearm, 39.5; greatest length of skull, 14.4; condylobasal length, 13.4; length of maxillary toothrow, C-$M^3$, 5.5; postorbital constriction, 3.9; zygomatic breadth, 8.7; breadth of braincase, 6.9; alveolar breadth across upper canines, 3.6; breadth across $M^3$-$M^3$, 5.7.

*Remarks*: This species is here recorded for the first time north of Panama (Handley, 1966). The bat was shot at night while it was hawking insects over the highway.

This specimen is listed without subspecific designation due to the lack of a sufficiently large series for proper comparison with South American forms (see further Handley, 1966).

### **Eptesicus furinalis gaumeri** (J. A. Allen)

*Adelonycteris gaumeri* J. A. Allen, 1897, Bull. Amer. Mus. Nat. Hist., 9: 231.
*Eptesicus albigularis,* Goodwin, 1942, Amer. Mus. Novitates, No. 1199, p. 1 (not *Vesperus* (*Marsipolaemus*) *albigularis* Peters, 1872).
*Eptesicus brasiliensis propinquus,* Dalquest, 1953, Louisiana State Univ., Bio. Sci. Ser., 1: 55 (not *Vesperus propinquus* Peters, 1872).
*Eptesicus gaumeri gaumeri,* Davis, 1965, Jour. Mamm., 46: 233.
*Eptesicus furinalis gaumeri,* Davis, 1966, Southwest. Nat., 11: 268.

*Specimens*: ALAJUELA: 8.4 miles from bridge at Atenas on road to San Matéo, 671 m, 1 ♂. LIMON: Finca La Lola, 50 m, 1 ♂; Tortuguero, sea level, 1 ♂ (UF 8025). PUNTARENAS: Boca de Barranca, sea level, 2 ♂♂, 3 ♀♀.

*Measurements*: (Averages and ranges): forearm (5 males, 3 females), 38.8 (37.8-39.6); (cranial, 3 males, 3 females) greatest length of skull, 15.7 (15.6-15.9); condylobasal length, 14.4 (14.1-14.8); length of maxillary toothrow, C-$M^3$, 5.6 (5.3-5.9); postorbital constriction, 3.8 (3.6-3.9); zygomatic breadth (2 males, one female, this measurement only), 10.5 (10.4-10.6); breadth of braincase, 7.3 (7.1-7.5); mastoid breadth, 8.2 (8.0-8.4); alveolar breadth across upper canines, 4.6 (4.4-4.9); breadth across $M^3$-$M^3$, 6.5 (6.3-6.6).

*Remarks*: Davis (1966) gives the range of this subspecies essentially as lowland Middle America and Caribbean South America, from Mexico to Surinam, and lists specimens (Davis, 1965) from every Middle American

country except Belize and Costa Rica. The records reported here serve to fill in the distribution of this bat on both lowlands of Costa Rica.

The specimens from Boca de Barranca were caught in mist nets set along the edge of a creek, along with *Rhynchonycteris, Rhogeëssa tumida, Molossus* sp. and several species of phyllostomatids; the one from the road to San Mateo was shot over the road at night not far from the locality at which *Peropteryx macrotis* and *Pteronotus davyi* were collected. The flight of *E. f. gaumeri* is quite similar to that of *Myotis nigricans.*

### **Eptesicus andinus** J. A. Allen

*Eptesicus andinus* J. A. Allen, 1914, Bull. Amer. Mus. Nat. Hist., 33: 382.
*Eptesicus chiriquinus* Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, 5: 362.
*Eptesicus brasiliensis andinus,* Hershkovitz, 1949, Proc. U.S. Nat. Mus., 99: 451.
*Eptesicus andinus andinus,* Davis, 1965, Jour. Mamm., 46: 239.
*Eptesicus andinus,* Davis, 1966, Southwest. Nat., 11: 252.

*Specimens*: SAN JOSE: San José, campus Universidad de Costa Rica, 1200 m, 1 ♀; Candelaria, elevation uncertain, 1 ♀ (MCZ 20445); Cerro de la Muerte, S restaurant "La Georgina" along Interamerican Highway, 4.2 miles, 2743 m, 2 ♂♂, 6.0 miles, 2590 m, 1 ♂, 6.8 miles, 2500 m, 2 ♂♂, and 17.5 miles, 1525 m, 1 ♂; San Isidro del General, 705 m, 1 ♀.

*Measurements*: (Averages and ranges) forearm (5 males, 3 females), 44.2 (42.8-46.4); greatest length of skull (6 specimens), 17.0 (16.7-17.3); condylobasal length (8), 16.0 (15.5-16.4); length of maxillary toothrow, C-$M^3$ (8), 6.2 (5.9-6.5); postorbital constriction (8), 4.1 (3.8-4.5); zygomatic breadth (7), 11.2 (10.9-11.6); breadth of braincase (7), 7.8 (7.7-8.1); mastoid breadth (7), 8.9 (8.4-9.2); alveolar breadth across upper canines (8), 5.0 (4.8-5.3); breadth across $M^3$-$M^3$ (8), 7.9 (6.9-7.3).

*Remarks*: The LACM specimens have been cited by Davis in his review of South American *Eptesicus* (1966); the one from Candelaria (MCZ) represents a new record. Only one locality north of Costa Rica is reported, based on one specimen from Chiapas, Mexico (Davis, 1966).

The animals from Cerro de la Muerte were all shot over the highway at night; that from San José (previously reported as *E. chiriquinus* by Tamsitt and Valdivieso, 1961) was taken in a mist net set across a small stream. Also captured in the same net with the latter specimen were *Eptesicus fuscus miradorensis, Myotis nigricans,* and several species of phyllostomatids. The *E. andinus* from Candelaria was part of a series of bats collected by C. F. Underwood, presumably all from the same locality, which included also an adult male *E. fuscus miradorensis* and a number of subadults and juveniles of the latter species.

### **Rhogeesa tumida tumida** H. Allen

*R* [*hogeësa*] *tumida* H. Allen, 1866, Proc. Acad. Nat. Sci. Phila, 18: 285.

*Rhogeëssa parvula tumida,* Hall, 1952, Univ. Kans. Publ., Mus. Nat. Hist., 5: 231.

*Rhogeëssa tumida tumida,* Goodwin, 1958, Amer. Mus. Nov., No. 1923: 3.

*Specimens*: GUANACASTE: Sámara, sea level, 2 ♀♀; PUNTARENAS: Boca de Barranca, sea level, 1 ♂; Hacienda Bonilla (near Boca de Barranca), sea level, 1 ♀.

*Measurements*: Forearm (male, 3 females, respectively), 29.2, 29.2, 29.3, 29.4; (cranial, male, first 2 females) greatest length of skull, 12.7, 12.8, 12.5; condylobasal length, 11.6, 11.4, 11.6; length of maxillary toothrow, C-$M^3$, 4.4, 4.4, 4.4; postorbital constriction, 3.2, 3.4, 3.1; zygomatic breadth, ——, 8.1, ——; breadth of braincase, 5.9, 6.0, 5.8; mastoid breadth, 6.7, 6.8, 6.8; alveolar breadth across upper canines, 3.7, 3.6, 3.6; breadth across $M^3$-$M^3$, 5.2, 5.4, 5.3.

*Remarks*: This tiny bat is known from Costa Rica from Miravalles, Prov. Guanacaste, (Sanborn, 1932), and "Pacific Coast" (Goodwin, 1946), in addition to the two localities recorded here. It has been taken in most countries of Central America (Goodwin, 1958; Handley, 1966). Our specimens are in agreement with the description and measurements of *R. t. tumida* published by Goodwin (1958). All four were caught in mist nets in association with several species of phyllostomatids.

### **Lasiurus ega panamensis** (Thomas)

*Dasypterus ega panamensis* Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, 8: 246.

*Lasiurus ega panamensis,* Handley, 1960, Proc. U.S. Nat. Mus., 112: 474.

*Specimens*: PUNTARENAS: Interamerican Highway, near bridge over Río Puerto Nuevo, *90 m*, 1 ♀, and near bridge over Río Catarata, 180 m, 1 ♂.

*Measurements*: (Male, female, respectively) forearm, 44.5, 45.9; greatest length of skull, 15.8, 16.2; condylobasal length, 14.5, 15.4; length of maxillary toothrow, C-$M^3$, 5.5, 5.6; postorbital constriction, 4.6, 4.4; zygomatic breadth, 10.3, 10.8; breadth of braincase, 8.4, 8.2; alveolar breadth across upper canines, 5.9, 6.0; breadth across $M^3$-$M^3$, 7.1, 7.4.

*Remarks*: The yellow bat is poorly represented from Central America. Only two specimens, both males, have been reported from Costa Rica, one from San José, Prov. San José, and the second from "Lajas Villa Quesada," Prov. Alajuela (Goodwin, 1946). The two individuals recorded here were both shot at night over the road, where they passed as they flew hunting patterns along the edge of the gorge of the Río Térraba. These bats were extremely rapid and maneuverable and they made considerable effort to stay out of our lights. In two nights of shooting at a fair number of yellow bats we were able to secure only these two specimens.

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# *PHOTONECTES MUNIFICUS,* A NEW SPECIES OF MELANOSTOMIATID FISH FROM THE SOUTH PACIFIC SUBTROPICAL CONVERGENCE, WITH REMARKS ON THE CONVERGENCE FAUNA

*By* ROBERT H. GIBBS, JR.

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# *PHOTONECTES MUNIFICUS,* A NEW SPECIES OF MELANOSTOMIATID FISH FROM THE SOUTH PACIFIC SUBTROPICAL CONVERGENCE, WITH REMARKS ON THE CONVERGENCE FAUNA

*By* Robert H. Gibbs, Jr.[1]

Abstract: *Photonectes munificus,* a new species in the stomiatoid family Melanostomiatidae, is described from a single specimen from the Subtropical Convergence of the South Pacific. The holotype, 371 mm standard length, is the largest ever recorded for the genus and is distinguished from other species by the highest IV and OV photophore counts (49-50 and 38), the lowest VAL count (2-4), and the greatest number of vertebrae (67). It most closely resembles species in the subgenus *Trachinostomias,* which have the dorsal and anal fins covered with black skin, and especially *P.* (*T.*) *margarita,* which, like *P. munificus,* often lacks the pectoral fin. A distinct circumglobal Subtropical Convergence fauna is characterized by nine restricted species of stomiatoids, and *P. munificus* is attributed to it.

A specimen of the genus *Photonectes,* collected in the Subtropical Convergence during cruise 24 of the *USNS Eltanin,* is the largest ever recorded for the genus and represents a previously undescribed species. Although there is confusion regarding the species of *Photonectes,* I have completed enough of a revisionary study to assure the validity of the new species.

## **Photonectes munificus** new species

Fig. 1

*Holotype*—Los Angeles County Museum of Natural History (LACM) 11282-1; female, 371 mm standard length. USNS ELTANIN, USC Station 1777; 41°50′S, 130°12′W to 41°46′S, 130°16′W; 14 August 1966. Ten-foot (3m) Isaacs-Kidd midwater trawl, surface to maximum depth of ca. 440 m. Local time 2050-2317 hours, two hours at depth.

*Diagnosis*—Dorsal and anal fins covered with black skin; pectoral fin absent; IV photophores 49-50; OV 38; VAL 2-4; vertebrae 67.

*Description* (most characters in Diagnosis not repeated)—Dorsal rays 19, the first small, the last split to the base; anal rays 21, the first tiny, the last split to the base (dorsal and anal rays counted from radiograph); pelvic rays 7. Serial photophores: IV 49 (left side), 50 (right side), those on isthmus not forming a separate group, the last three before the pelvics close together; VAV 12, anterior three and posterior four forming close groups; AC 12, the first four close together, next four more widely spaced, last four gradually becoming

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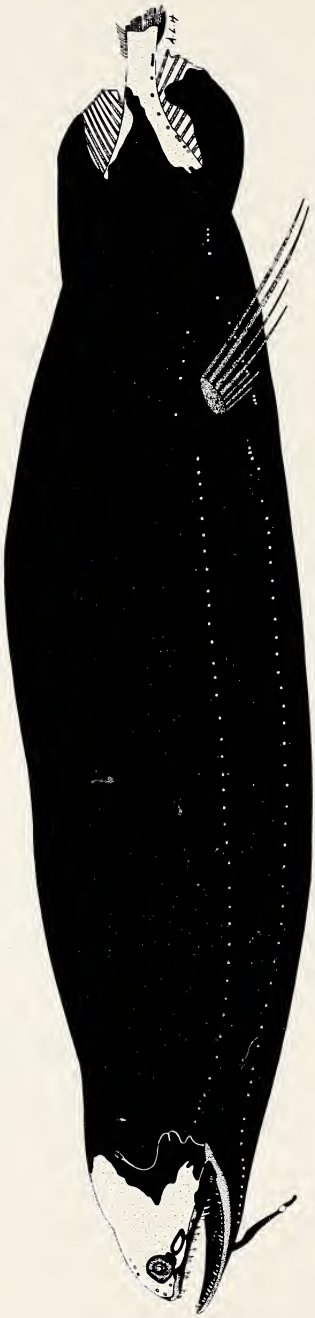

Figure 1. Holotype of *Photonectes munificus*, LACM 11282-1, 371 mm. Pale areas on the head and posterior end are due to removal of skin. Drawn by Ann Hoskins.

smaller and closer together; OV 38; VAL 4 (left side), 2 (right side), widely spaced, the last well anterior to anal-fin origin. Branchiostegal photophores 9. Vomerine teeth, one on each side. Palatine teeth, 3 on each side. Gill teeth 9, single, on lower limb only.

*Measurements* (in mm; percent of standard length in parentheses)—standard length 371; snout to dorsal origin 300.1 (80.7); snout to anal origin 313.1 (84.2); snout to pelvic insertion 258.3 (69.5); head length 49.1 (13.2); snout to anterior bony margin of orbit 8.9 (2.4); fleshy orbit length 7.0 (1.9); postocular organ, pale part only 4.0 (1.1), entire black surrounding area 6.9 (1.9); upper jaw length 43.3 (11.6); body depth behind head 48.8 (13.1); greatest body depth 77.4 (20.8); least caudal peduncle depth 8.2 (2.2); pelvic fin length 91.4 (24.6); length of dorsal fin base 51.4 (13.8); length of anal base 51.5 (13.9).

Barbel with a small bulb, but broken distally; length to end of bulb 19.0 (5.1), length to broken end 22.3 (6.0).

No luminous tissue in mouth, on jaws, or on body.

Orangish eggs present, about 0.35 mm in diameter.

*Relationships*—The new species, *P. munificus,* is obviously closely related only to those species included in the subgenus *Trachinostomias* Parr by Morrow (in Morrow and Gibbs, 1964), who revised the subgeneric classification of Regan and Trewavas (1930). These species—*P. bifilifer* Beebe, *P. fimbria* Regan and Trewavas, *P. parvimana* Regan and Trewavas, and *P. margarita* (Goode and Bean)—are characterized by dorsal and anal fins that are more or less completely covered with thick black skin, by the highest IV and OV photophore counts within the genus (total range 41-48 and 30-36 respectively), and by the highest vertebral number (the highest so far counted, either in the literature or on my numerous radiographs, is 64). The previous maximum photophore and vertebral counts in the genus *Photonectes* are, thus, exceeded by several in *P. munificus,* while the VAL count of 2-4 is much lower than the previously recorded minimum of 10 for the genus. Because pectoral fins are absent in *P. munificus,* a relationship with species of the subgenera *Photonectes* Günther and *Dolichostomias* Parr, which also lack pectorals, might be considered. Pectoral fin development in the genus *Photonectes,* however, is weak in all species, and *P. margarita* (subgenus *Trachinostomias*) may have one ray, ranging from long to very short, or may lack the ray on one or both sides. The sole known representative of the subgenus *Dolichostomias, P. gracilis,* is well-differentiated. It is generally more slender than other *Photonectes,* has the pelvic fins inserted before the mid-length, and has long dorsal and anal fin bases. I believe that *P. munificus* is closest to *P. margarita.*

*Distribution*—The capture of *P. munificus* at a depth of 0-440 m in the Subtropical Convergence suggests that this new species is a member of the fauna of the Convergence, a fauna that I believe constitutes a distinct zoogeographic region encircling the Southern Ocean. The same trawl collected *Bathophilus ater* (Brauer), another stomiatoid species of similar zoogeographic pro-

pensities. Brauer (1902) described *B. ater* from 26°49′S, 5°54′E, and M.A. Barnett and I have examined other specimens from between 27°10′S and 32°29′S, all in the southeastern Atlantic. Specimens of *B. ater* from cruises of the Eltanin show this species to occur all across the south Pacific from New Zealand to Chile at latitudes between 33° and 45° S.

Very few species of stomiatoid fishes occur south of the limits of the great central water masses or the waters underlying these water masses and fewer still are restricted to the far southern waters. I am aware of 17 species that have the Subtropical Convergence as the southern boundary of a widespread distribution (Table 1). *Stomias gracilis* is the only stomiatoid that, to my knowledge, is found only in subantarctic and antarctic waters; it is replaced by *S. boa boa* in the Subtropical Convergence. *Borostomias antarcticus,* an antitropical species, and *Idiacanthus atlanticus* occur in the Convergence and in more southern waters as well. Nine species of stomiatoids appear restricted to the Subtropical Convergence (Table 1), ten if *Photonectes munificus* is included. But for a recent capture in the central Atlantic, *Trigonolampa miriceps* might also be considered an antitropical member of the Convergence fauna.

Further collecting and study will doubtless confirm the reality of a Subtropical Convergence fauna. With regard to *Photonectes munificus,* I predict that future collecting will show this species to occur around the world in the Convergence and northward into the southern reaches of the Benguela and Humboldt currents.

*Etymology*—The specific name *munificus,* is a Latin adjective meaning bountiful, used in reference to the high meristic counts of the species and the large body size of the holotype.

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TABLE 1

Stomiatoid genera and species represented in the Subtropical Convergence and/or in subantarctic waters. Approximate total number of species in each genus in parentheses. SA—species occurring in subantarctic waters. CONVERGENCE—species occurring only in the Convergence (x) or also in subantarctic waters (o). S. LIMIT—species known from central waters that occur in the Convergence area. SOURCES—1. R. H. Gibbs *et al.*, unpublished; 2. W. H. Krueger, unpublished; 3. this paper; 4. Barnard, 1948; 5. Brauer, 1906; 6. Bussing, 1965; 7. Ege, 1934; 8. Ege, 1948; 9. Gibbs and Hurwitz, 1967; 10. Günther, 1887; 11. Morrow, 1964; 12. Norman, 1930. A—Atlantic Ocean. I—Indian Ocean. P—Pacific Ocean.

| Genus and Species | SA | Convergence | | | S. Limit | | | Source |
|---|---|---|---|---|---|---|---|---|
| | | A | I | P | A | I | P | |
| *Chauliodus* (6) | | | | | | | | |
| *sloani* | | | | | | x | | 9 |
| *danae* | | | | | x | | x | 6,8 |
| *Stomias* (9) | | | | | | | | |
| **boa boa* | | x | x | x | | | | 1,7 |
| *gracilis* | x | | | | | | | 1,7 |
| *Macrostomias* (1) | | | | | | | | |
| *longibarba* | | | | | x | x | | 1,11 |
| *Astronesthes* (23) | | | | | | | | |
| *boulengeri* | | x | x | x | | | | 1 |
| sp. nov. | | | x | x | | | | 1 |
| *indicus* | | | | | | | x | 1 |
| *Borostomias* (5) | | | | | | | | |
| *antarcticus* | x | o | o | o | | | | 1 |
| *Neonesthes* (2) | | | | | | | | |
| *capensis* | | | | | x | x | x | 1 |
| *microcephalus* | | | | | | x | x | 1 |
| *Eustomias* (35) | | | | | | | | |
| *trewavasae* | | x | x | x | | | | 1 |
| *enbarbatus* | | | | | | x | | 1 |
| *Flagellostomias* (1) | | | | | | | | |
| *boureei* | | | | | x | | | 12 |

**S. boa boa* also has a disjunct population in the Mediterranean Sea and the adjacent eastern Atlantic.

TABLE 1 (continued)

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Leptostomias* (11) | | | | | | | | | | |
| *macropogon* | | | | | | | x | | | 12 |
| *gladiator* | | | | | | | | x | | 1 |
| *Bathophilus* (18) | | | | | | | | | | |
| *ater* | | | x | | x | | | | | 1,5 |
| *irregularis* | | | | | | | x | x | | 1,12 |
| *pawneei* | | | | | | | x | | | 1,12 |
| *nigerrimus* | | | | | | | x | | | 1 |
| *Echiostoma* (1) | | | | | | | | | | |
| *barbatum* | | | | | | | x | | | 1 |
| *Melanostomias* (7) | | | | | | | | | | |
| *tentaculatus* | | | | | | | x | | | 1,12 |
| *Thysanactis* (1) | | | | | | | | | | |
| *dentex* | | | | | | | | x | | 1 |
| *Opostomias* (2) | | | | | | | | | | |
| *micripnus* | | | x | x | x | | | | | 1,4,10 |
| *Photonectes* (15) | | | | | | | | | | |
| *munificus* | | | | | x | | | | | 3 |
| *Trigonolampa* (1) | | | | | | | | | | |
| *miriceps* | | | | | | | | x | x | 1 |
| *Idiacanthus* (3) | | | | | | | | | | |
| *atlanticus* | x | | o | o | o | | | | | 2 |
| *Malacosteus* (1) | | | | | | | | | | |
| *niger* | | | | | | | x | x | | 1 |
| Total Species 142 | 3 | | | 9 | | | | 17 | | |

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# CHIGGERS OF THE GENUS *PSEUDOSCHOENGASTIA* (ACARINA: TROMBICULIDAE) FROM COSTA RICA

*By* JULIUS C. GEEST AND RICHARD B. LOOMIS

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DOROTHY M. HALMOS
*Editor*

# CHIGGERS OF THE GENUS *PSEUDOSCHOENGASTIA* (ACARINA: TROMBICULIDAE) FROM COSTA RICA

*By* JULIUS C. GEEST[1] AND RICHARD B. LOOMIS[1]

ABSTRACT: Chigger larvae of thirteen species of the genus *Pseudoschoengastia* are described and reported from mammals of Costa Rica. Nine species are new and the other four are recorded from this country for the first time. The subgenus *Pseudoschoengastia* Lipovsky contains ten species: *P. bulbifera* Brennan, *P. intermedia* sp. n., *P. montana* sp. n., and *P. peromysci* sp. n. belonging to the Bulbifera Complex of the Hungerfordi Group; *P. zona* Brennan, *P. hoguei* sp. n., *P. hooperi* sp. n., and *P. rheomys* sp. n. of the Farneri Group; *P. abditiva* Brennan and *P. finitima* Brennan and Yunker in the Anomala and Aeci Groups respectively. The second subgenus, *Walchioides* Vercammen-Grandjean, has three new species: *P. costaricensis, P. guanacastensis* and *P. verdensis.*

These chiggers were found on fifteen species of rodents: *Heteromys desmarestianus, Liomys salvini, Oryzomys* (five species), *Ototylomys phyllotis, Peromyscus nudipes, Rheomys hartmanni, Rheomys underwoodi, Scotinomys teguina, Sigmodon hispidus, Zygodontomys microtinus* and *Proechimys semispinosus*; and on one opossum *Philander opossum.*

Species of *Pseudoschoengastia* are recorded from 24 localities. The life zones, biotic provinces and biotic districts of Costa Rica are discussed and mapped. Three species are limited to the Guanacaste Biotic District of the Pacific México-Nicaragua Biotic Province and two species are known from the Golfo Dulce Biotic District of the Pacific Costa Rica-Panamá Biotic Province, both along the Pacific versant. Two species occur in the Caribbean Costa Rica Biotic District of the Caribbean Costa Rica-Panamá Biotic Province, also of the Tropical Lowlands. Nine species occur in the Tropical Highlands or Costa Rica-Panamá Highlands Biotic Province, which is divided into the Costa Rica Highlands Biotic District in the north with six species and the southern Panamá Highlands Biotic District, also with six species of *Pseudoschoengastia.*

The larval stage of each species is described and illustrated, and notes are given on the ecology, including a complete host list. A key is included to the larvae of the twenty species of *Pseudoschoengastia* known from Central and South America.

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collect mammals and their ectoparasites and to observe the various habitats in Costa Rica for a period of six months.

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## INTRODUCTION

Chiggers of the genus *Pseudoschoengastia* Lipovsky belong to the subfamliy Trombiculinae, family Trombiculidae. As larvae, they possess six legs and parasitize small mammals, especially rodents. Both the taxonomy and classification have been based on the larvae, the only stage easily obtained. The nymphs and adults are free-living and have not been taken in Costa Rica.

From January, 1962, to December, 1964, more than 500 rodents from Costa Rica were examined and chiggers were recovered from approximately 291 specimens. Of those with chiggers, 112 hosts (nearly 39 percent) had one or more species of *Pseudoschoengastia.* These larvae were recovered from the ears of 16 host species, including one opossum and 15 kinds of rodents belonging to three families: Heteromyidae, Cricetidae, and Echimyidae.

Examination of 548 larvae revealed 13 species of *Pseudoschoengastia,* nine of which are new; ten species in the subgenus *Pseudoschoengastia* Lipovsky, and three species in the subgenus *Walchioides* Vercammen-Grandjean.

## DESCRIPTION OF COSTA RICA

Costa Rica is a small Central American Republic with numerous volcanoes, high mountains, plateaus and coastal plains providing diverse habitats for many kinds of plants and animals. Physiographically Costa Rica consists

of Pacific and Atlantic lowlands almost completely separated by central highlands, which follow roughly a northwest to southeast orientation.

The Pacific lowland is widest at the Nicoyan Peninsula in Guanacaste Province, and after narrowing near mid-country, widens again in the region of Golfo Dulce and the Osa Peninsula. The Atlantic lowland extends almost entirely across the northern border but narrows to less than 50 kilometers at the Panamanian border.

The elevation near the Nicaraguan border is no greater than 100 meters; however, just to the south is the Cordillera de Guanacaste with elevations over 1000 meters. This range consists of a series of volcanoes called the Cordillera Volcánica, and at the southern end is the east-west range, the Cordillera Central. Here the lowest elevation is 1500 meters, but between Volcán Irazú and Volcán Turrialba the lowest elevation is 2150 meters. To the south, the Cordillera Central forms the central plateau, or Meseta Central, which separates the northern and southern highlands. South of this plateau is the Dota Region, the lower northern portion of the Cordillera de Talamanca, which for one hundred and sixty kilometers forms the major northwest-southeast axis with elevations above 2150 meters.

The following numbered localities for *Pseudoschoengastia* are plotted in Figs. 1 and 2 and are listed consecutively from northwest to southeast:

GUANACASTE PROVINCE: 1. 5-8.3 km N Liberia; 2. Liberia; 3. 1.4 km S and 7.3 km S Liberia; 4. 3 km S Playa del Coco; 5. 5 km NW Tilarán. PUNTARENAS PROVINCE: 6. Monteverde, 1380 m. HEREDIA PROVINCE: 7. 2.9 km S Puerto Viejo; 8. El Angel Falls. ALAJUELA PROVINCE: 9. Volcán Poás, 2493 m, and Rió Poasito, Poasitos, 2000 m. CARTAGO PROVINCE: 10. Río Claro, 600 m, 27.5 km N San José on San Jerónimo Rd. LIMON PROVINCE: 11. Finca "La Lola." CARTAGO PROVINCE: 12. Turrialba, IICA, 600 m; 13. Tapanti, Río Quiri, 1220 m. SAN JOSE PROVINCE: 14. Río Damitos, 14 km N Quepos; 15. 11.3 km S La Georgina, 2500 m; 16. 15-20.8 km N San Isidro del General, 1495-1600 m. PUNTARENAS PROVINCE: 17. Finca "Los Helechales," 12-15 km E Potrero Grande, 1040 m; 18. Finca de Señor Treno, 8 km E Potrero Grande, 660 m; 19. 1.7 km W Palmar Norte; 20. Río Coronado, 20 km N Puerto Cortez; 21. 7.3 km S Palmar Sur; 22. Rincón de Osa, 50 m; 23. 8.3 km W Rincón, Camp Seattle, 100 m; 24. vicinity of Villa Neily.

## LIFE ZONES

The five life zones and the forest formations in the Tropical Life Zone, as discussed and mapped by Slud (1964), are listed below.

I. Tropical Life Zone.
   - A. Tropical Dry Forest Formation
   - B. Moist Forest Formation
   - C. Tropical Wet Forest Formation

II. Subtropical Life Zone.

III. Submontane Life Zone.
IV. Montane Life Zone.
V. Subalpine Life Zone.

The map (Fig. 2) follows Slud except that the Tropical Wet and Moist Forest Formations are combined and the Subalpine Life Zone is not shown. This latter Life Zone is surrounded by the Montane Life Zone and occurs on two mountain tops where no *Pseudoschoengastia* are found.

## BIOTIC PROVINCES AND BIOTIC DISTRICTS

Many authors have stated that Costa Rica can be divided into areas based on the distribution of plants and animals and on the environmental factors. Goodwin (1946), in discussing mammalian distributions, did not delineate distinct provinces but mentioned five regions. Taylor (1951) suggested essentially the same patterns of distribution based upon the herpetofauna. Slud (1964) proposed, but did not map, four distinct avifaunal zones based on the geography, climate, geologic history, and the distribution of birds.

Although he stated that there were differences in the compositions of bird species between the two major mountain areas, he found it convenient to keep them together as a single avifaunal zone. Slud utilized plant data adapted from Holdridge (1959) to give more definite boundaries to his avifaunal zones. West (1964) listed four "natural regions" that seem to correspond to the avifaunal zones of Slud. Ryan (1963) utilized the distribution of mammals to define the biotic provinces of Central America. He divided Costa Rica into two provinces, the Puntarenas-Chiriquí Biotic Province of the Pacific slope and the Guatuso-Talamancan Biotic Province of the Caribbean slope, separated by the central highlands. Ryan did not believe that the highlands should be a separate biotic province, and both the northern dry and southern wet forests of the Pacific slope were placed into one province. This arrangement does not seem as appropriate for Costa Rica as that of Stuart (1964), who mapped and named the biotic provinces of Central America, including four biotic provinces within Costa Rica, based upon the flora and the known vertebrate and invertebrate faunas. These biotic provinces are comparable to the avifaunal

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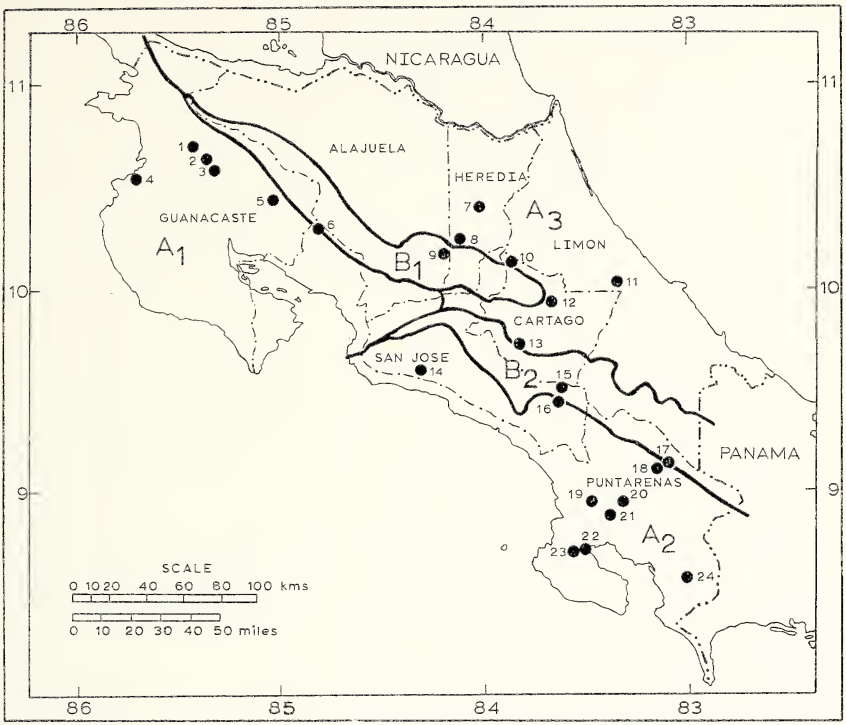
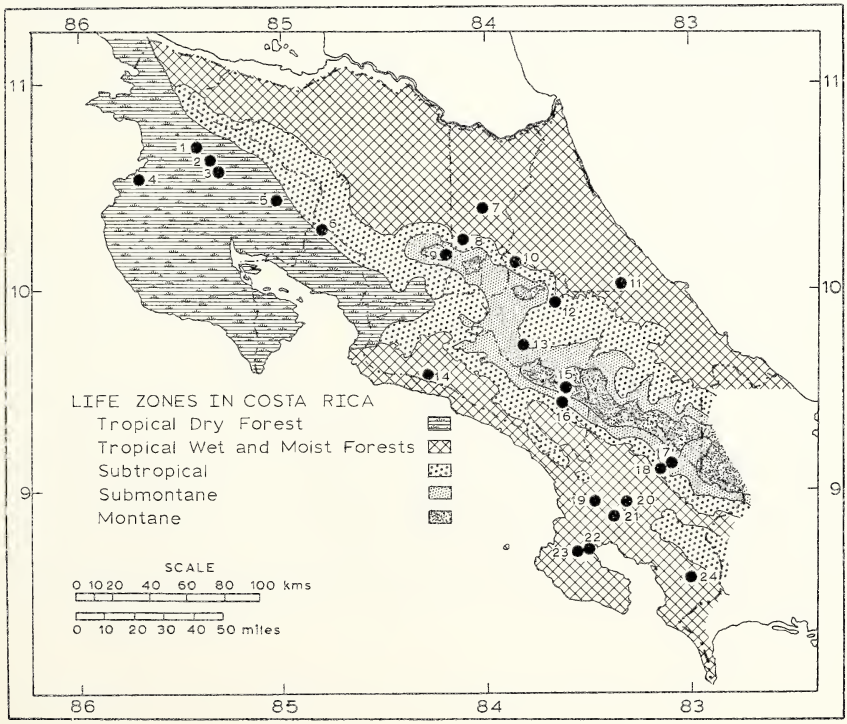
Figure 1. Map of Costa Rica showing Biotic Provinces and Districts, political provinces and all localities for *Pseudoschoengastia*. Localities 1-24 are listed in the text.
A. Tropical lowlands
A1. Guanacaste Biotic District of the Pacific México-Nicaragua Biotic Province.
A2. Golfo Dulce Biotic District of the Pacific Costa Rica-Panamá Biotic Province.
A3. Caribbean Costa Rica Biotic District of the Caribbean Costa Rica-Panamá Biotic Province.
B. Tropical highlands (Costa Rica-Panamá Highlands Biotic Province)
B1. Costa Rica Highlands Biotic District.
B2. Panamá Highlands Biotic District.

Figure 2. Life Zones in Costa Rica and localities for *Pseudoschoengastia*.


NICARAGUA
ALAJUELA
HEREDIA
GUANACASTE
LIMON
CARTAGO
SAN JOSE
PUNTARENAS
PANAMA
A1
A2
A3
B1
B2
SCALE
0 10 20 40 60 80 100 kms
0 10 20 30 40 50 miles


LIFE ZONES IN COSTA RICA
Tropical Dry Forest
Tropical Wet and Moist Forests
Subtropical
Submontane
Montane
SCALE
0 10 20 40 60 80 100 kms
0 10 20 30 40 50 miles

zones of Slud. For zoogeographic patterns the biotic provinces, as originally conceived by Dice (1943), represent a more realistic picture than do life zones.

In a recent paper, Savage (1966:723) listed and mapped the Recent Central American Herpetofaunas. Four separate herpetofaunas were shown for Costa Rica. His Nicaraguan herpetofauna corresponds to our Guanacaste Biotic District, the Golfo Dulcean is the same as the Golfo Dulce Biotic District and the Isthmian has the same distribution as the Costa Rica Caribbean. Savage considered the tropical highlands as a single herpetofauna, the Talamancan. The entire Central American Region is called Mesoamerica, which extends northward to the Nearctic in México and southward to the Neotropical of eastern Panamá and South America.

The following biotic provinces and districts are used to aid in the understanding of the distribution of *Pseudoschoengastia* and their mammalian hosts. The names assigned to the four biotic provinces presented below, and shown in Fig. 1, follow Stuart (1964). In addition, we have subdivided these biotic provinces of Costa Rica into biotic districts, and each is given an appropriate name.

The Tropical Lowlands (A) consists of the Pacific Mexico-Nicaragua Biotic Province and its Guanacaste Biotic District (A1); the Pacific Costa Rica-Panamá Biotic Province and its Golfo Dulce Biotic District (A2); the Carribbean Costa Rica-Panamá Biotic Province with its Caribbean Costa Rica Biotic District (A3).

The Tropical Highlands (B) is composed of the Costa Rica-Panamá Highlands Biotic Province subdivided into the Costa Rica Highlands Biotic District (B1) and the Panama Highlands Biotic District (B2).

Rainfall data presented under each biotic province and district were taken from the official records of the Ministerio de Agricultura y Ganadería, Seccion Climatológia, for 1961.

## PACIFIC MEXICO-NICARAGUA BIOTIC PROVINCE
## GUANACASTE BIOTIC DISTRICT

The Pacific México-Nicaragua Biotic Province, as represented in Costa Rica, is called the Guanacaste Biotic District. It covers the northern half of the Pacific slopes of Costa Rica and includes the Tropical and Subtropical Life Zones. It is the southern part of a relatively arid Pacific Coast forest which extends intermittently from the state of Sinaloa, México, southward to the mouth of the Gulf of Nicoya (Slud, 1964). The Guanacaste Biotic District is named for the large political province which is the major part of the district.

The average annual rainfall in 1961 for ten stations was less than 2000 mm and most of this was concentrated during the months of June through November with over 50 mm of rainfall recorded for each of these months. Taylor (1951) stated that the rainfall is confined for the most part to the summer months (May to August), while the remaining months have little or

no rainfall and the winds during this dry season contribute to further moisture loss for this already dry area.

Although many areas with better soil have been cleared and burned, it originally supported subhumid to moist forest associations with tall stands of deciduous forest composed of relatively few species (Slud, 1964).

The mammals (Goodwin, 1946) and birds (Slud, 1964) of this region are primarily northern in origin. Three new chigger species, *Pseudoschoengastia hoguei, P. costaricensis* and *P. guanacastensis,* occur only in this biotic district.

### PACIFIC COSTA RICA-PANAMA BIOTIC PROVINCE
### GOLFO DULCE BIOTIC DISTRICT

That part of the Pacific Costa Rica-Panamá Biotic Province in Costa Rica includes the Pacific versant from the southern tip of the Nicoyan Peninsula into Panamá. The Tropical and parts of the Subtropical Life Zones are included in this district.

In 1961, the average rainfall of ten stations was in excess of 3500 mm, with one station recording more than 7200 mm. All months except January (85 mm) and February (36 mm) had rainfall in excess of 100 mm.

The forest association is composed predominantly of tall evergreen species typical of the tropical humid to wet rainforest. On good undisturbed soils, approximately 100 species of trees make up this three or four story tropical rain forest. The canopy is almost closed and the crowns of the scattered emergents project above it. The forest floor has only a small amount of litter and the easy passage through this forest reveals buttressed trunks of the larger trees, stilt roots of the smaller trees, and the presence of many lianas, as mentioned by Allen (1956).

Slud (1964) stated that many birds of this region can tolerate the humid conditions on both the eastern and western slopes, although the many endemics found here and the absence of Caribbean species attest to a distinct avifauna.

Two species of *Pseudoschoengastia* occur in this district. *Pseudoschoengastia bulbifera* has been taken at seven of the eight localities, and *P. zona* is known from one locality.

### CARIBBEAN COSTA RICA-PANAMA BIOTIC PROVINCE
### CARIBBEAN COSTA RICA BIOTIC DISTRICT

This district extends along the entire length of the eastern slope, and includes the Tropical and Subtropical Life Zones.

The average annual rainfall in 1961 at ten stations was in excess of 3400 mm. Yearly rainfall in excess of 7200 mm has been recorded in the extreme northeastern corner. The average recorded rainfall for each month in 1961 was in excess of 100 mm. There was less rainfall in January (102 mm) and February (170 mm) and a second relatively "dry spell" occurred from Septem-

ber to November, as each month had less than 300 mm of rainfall.

The evergreen floral composition of this biotic district has extremely moist to wet forest associations similar to those found in the Golfo Dulce Biotic District. The lower slopes near sea level are covered by extensive tracts of palm swamps that are almost impassable because of numerous water courses and a year-round high water table. Large tracts of this land in Costa Rica and Panamá have been cleared to grow bananas, cacao and sugar cane. Many typical species of trees in the Golfo Dulce Biotic District are also found here. Slud (1960, 1964) listed the species of trees.

Goodwin (1946) stated that the mammals of the Caribbean are closely related to forms in adjacent Panamá, and Slud (1964) noted that affinities of the Caribbean species of birds are with species of Panamá and South America.

Of the two species of *Pseudoschoengastia* taken in this district, *P. bulbifera* were taken from all localities and *P. finitima* from only one site.

### Costa Rica-Panama Highlands Biotic Province

This biotic province of the Tropical Highlands in Costa Rica consists of two distinct areas which are separated into the northern Costa Rica Highlands and the southern Panamá Highlands Biotic District. Seven of the nine species of *Pseudoschoengastia* from this province have not been taken elsewhere, but only *P. montana* sp. n. is known from both districts.

### Costa Rica Highlands Biotic District

This biotic district, with many endemic species of mammals (Goodwin, 1946), consists of the northern mountains and Cordillera Central, including the Montane, Submontane and parts of the Subtropical Life Zones.

The average annual rainfall in 1961 for ten stations was in excess of 2600 mm. The rainfall pattern was similar to that of the adjacent Guanacaste Biotic District, although the rainfall was heavier and the pattern showed sharper peaks.

Slud (1964) stated that the evergreen trees of the subtropical forest often form a dense canopy but are not of value as timber and are poorly known. The montane moist to very humid forest formations are dominated by many species of oaks that are often bathed in clouds. Many of these temperate mountain areas have been cleared to raise fruits, vegetables, and cattle.

Goodwin (1946) believes that many mammals of this district have affiinities with species of the Mexican Central Plateau.

Six species of *Pseudoschoengastia* are reported; one new species (*P. montana*) is known only from these two highland districts, and three new species (*P. hooperi, P. peromysci,* and *P. verdensis*) were taken in this district.

### Panama Highlands Biotic District

This district is south of the central plateau and includes the mountains of

the north-central Dota Region of Costa Rica and the high Talamanca Cordillera. These mountains terminate with Cerro Pittier in the Chiriquí region of Panamá bordered by the arid savannas of northwestern Panamá. Subtropical to Subalpine Life Zones occur in this biotic district.

The average rainfall for eight stations was in excess of 2300 mm and had a pattern similar to that of the Costa Rica Highlands. The Panamá Highlands has fewer human inhabitants, and rainfall records probably are from the drier areas.

The moist to wet forest formations of this region are dominated by species of oaks and a subalpine wet páramo above the tree line on Cerro de la Muerte and Cerro Chirripó, which according to Slud (1964) has an affinity with the páramos of the Andes.

Most species of mammals (Goodwin, 1946) and birds (Slud, 1964) are related to forms of Panamá and South America.

Six species of *Pseudoschoengastia* have been taken here, of which three (*P. abditiva, P. intermedia* sp. n., and *P. rheomys* sp. n.) were not obtained elsewhere in Costa Rica.

TABLE 1

The distribution of *Pseudoschoengastia* in Costa Rica, based on the occurrence of the species in each biotic district. Numbers in each column refer to the number of localities for each species.

| | BIOTIC DISTRICTS | | | | |
|---|---|---|---|---|---|
| Species | A1 | A2 | A3 | B1 | B2 |
| Total localities with *Pseudoschoengastia* | 5 | 8 | 6 | 2 | 3 |
| 1. *P. bulbifera* Brennan | — | 7 | 6 | 1 | 2 |
| 2. *P. intermedia* sp. n. | — | — | — | — | 1 |
| 3. *P. montana* sp. n. | — | — | — | 1 | 2 |
| 4. *P. peromysci* sp. n. | — | — | — | 1 | — |
| 5. *P. zona* Brennan | — | 1 | — | 1 | 2 |
| 6. *P. hoguei* sp. n. | 3 | — | — | — | — |
| 7. *P. rheomys* sp. n. | — | — | — | — | 1 |
| 8. *P. hooperi* sp. n. | — | — | — | 1 | — |
| 9. *P. abditiva* Brennan | — | — | — | — | 1 |
| 10. *P. finitima* Brennan & Yunker | — | — | 1 | — | — |
| 11. *P. guanacastensis* sp. n. | 3 | — | — | — | — |
| 12. *P. costaricensis* sp. n. | 3 | — | — | — | — |
| 13. *P. verdensis* sp. n. | — | — | — | 1 | — |
| Number of species in each district (or districts) | 3 | 2 | 2 | 6 | 6 |
| | | 3 | | 9 | |
| Number limited to biotic district (in Costa Rica) | 3 | 0 | 1 | 3 | 3 |
| | | | | 1 | |

## MATERIALS AND METHODS

From 1962 through 1964 approximately 3,500 mammals from Costa Rica were examined for ectoparasites. Most of these were bats, but 505 were rodents. They were taken primarily in Sherman live traps, rat and museum special kill traps using baits of rolled oats, bananas and peanut butter.

Each specimen was sealed in a separate cloth or plastic bag until it was examined for ectoparasites with the aid of a stereoscopic microscope. The estoparasites were preserved in 75 per cent ethyl alcohol and each kind of parasite and its location on the host usually were listed in the field notes. The mammals were prepared as wet specimens in formalin or as dry study skins and have been deposited in the Los Angeles County Museum of Natural History (LACM).

Representatives of the larval chiggers were mounted in polyvinyl alcohol-lactophenol (PVA-LP). These larvae were studied with the aid of a phase-contract microscope, and all drawings, made with the aid of a drawing tube by the senior author, were based on the type series and other specimens from Costa Rica.

Specimens designated with an O- were taken by members of the LACM field parties and those specimens with the designation "RML" belong to the Rocky Mountain Laboratory, Hamilton, Montana. Unless otherwise noted, the chiggers have been deposited in the Acarina collection, LACM.

The holotype and at least one paratype of each new species has been retained in the LACM collection. When available, paratypes will be deposited in the following collections: Chigger Research Collection, California State College, Long Beach; Rocky Mountain Laboratory, Hamilton, Montana; The University of Kansas; The George Williams Hooper Foundation, University of California Medical Center, San Francisco; United States National Museum; Institute of Acarology, Ohio State University; Bishop Museum, Honolulu, Hawaii; Dr. Anita Hoffmann, Mexico, D.F., and other appropriate institutions and individuals.

## ACCOUNTS OF THE SPECIES

The terminology for the larva usually follows that of Wharton *et al.* (1951), supplemented by the terms from Newell (1957). All measurements are in microns. Unless otherwise noted, the description and illustrations of each new species are based upon the holotype. Paratypes from Panamá and referred specimens from Costa Rica were utilized to characterize those species already named. The term "group" is utilized to bring together similar species below the subgeneric level. Any subgroup of several more nearly similar and presumably related species is called a complex.

### Genus **Pseudoschoengastia** Lipovsky, 1951

*Type-species*: *Pseudoschoengastia hungerfordi* Lipovsky, 1951.

*Vanidicus* Brennan and Jones, 1961 (type species, *Vanidicus tricosus*), *new synonymy.*

*Pseudoschoengastia* was proposed by Lipovsky (1951) to include two new species, *P. hungerfordi* and *P. farneri,* and *Ascoschoengastia diazi* (Hoffmann 1948). Two additional species, *Ascoschoengastia anomala* and *A. pedregalensis,* were described from México by Hoffmann (1951), and Brennan (1952) named *P. guatemalensis* from Guatemala and *P. occidentalis* from California. Seventeen additional species of *Pseudoschoengastia* have been described from southwestern United States and from México southward to Panamá (Brennan and Jones, 1959; Brennan, 1960; Hoffmann, 1960; Brennan, 1965; Brennan and Yunker, 1966). Fauran (1960) described *Pseudoschoengastia myoproctae* from French Guiana, the only species of this genus known from South America.

Brennan and Jones (1961) described a new genus and species, *Vanidicus tricosus,* from Panamá, and indicated a close relationship to *Pseudoschoengastia.* The absence of differentiation in characters and the close similarity to *P. abditiva* Brennan has prompted us to synonymize *Vanidicus* with the genus *Pseudoschoengastia.*

*Walchioides* Vercammen-Grandjean (1960) was proposed originally as a subgenus of the Asiatic genus *Susa* Audy. Although the type-species, *Walchia gouldi* Hoffmann from México, is unique in lacking the AM scutal seta, it closely resembles several species of *Pseudoschoengastia,* and therefore we consider *Walchioides* a subgenus of *Pseudoschoengastia.* We are placing all species of *Pseudoschoengastia* with the PL setae on the scutal plate in the subgenus *Walchioides.*

Twenty-seven species of *Pseudoschoengastia* have been described: four from the United States; 13 from México and Guatemala; nine from Panamá; one from northern South America. The nine additional species from Costa Rica described below brings the total number to 36.

Larval *Pseudoschoengastia* are parasitic on small rodents, lagomorphs, insectivores and other small terrestrial mammals.

*Referred species*: Thirty-six species, arranged below in two subgenera: *Pseudoschoengastia* (26 species) and *Walchioides* (10 species).

*Diagnosis*: *Pseudoschoengastia* differs from all other genera in the subfamily Trombiculinae by having the following combination of larval characters: scutum small; sensilla clavate to capitate; palpotibial claw trifurcate; palpal tarsus with five branched setae; body with many setae, usually with two or more pairs of humeral setae and one or more pairs of lateral humeral and lateral sternal setae between coxae II and III; leg I with stout subterminala (dorsal eupathid) and parasubterminala (companion seta); basifemur and telofemur III completely or partially fused (showing line of previous articulation), with two or more internal bars; tibiala III present; leg III without mastisetae. Closely resembling the genera *Euschoengastoides* Loomis and *Cordiseta* Hoffmann; but differing from *Euschoengastoides* in having subterminala and parasubterminala I (usually absent in *Euschoengastoides*); lateral humeral and lateral sternal setae between coxae II and III (absent in *Euschoengas-*

*toides*); long slender vestigiala on leg I (short dagger-shaped vestigiala in *Euschoengastoides*); femora II and III fused (not fused in *Euschoengastoides*); differing from *Cordiseta* in lacking large foliate dorsal body setae.

*Description*: Larval characters as in diagnosis, plus: scutum with posterolateral setae on or off the scutal plate; expanded sensilla with setules large to extremely small; cheliceral blade with a terminal tricuspid cap (some with a serrated medial margin), and with or without a dorsomedial tooth; palpal tarsus without subterminala (eupathid); body small, ellipsoidal and somewhat constricted when engorged; eyes 2/2 (rarely absent), usually on a plate; anus at level of 4th and 5th rows of ventral body setae; postanal setae resembling dorsal setae; all legs terminating in two lateral claws and median clawlike empodium, without tenent hairs (onychotriches); cheliceral bases, capitular sternum, scutum and all leg segments punctate. Galeala usually nude, rarely with one to four fine branches.

*Comments*: There is some confusion in the names of the lateral body setae which are present between and near coxae II and III of *Pseudoschoengastia*. Lipovsky (1951) and Brennan (1952) followed Hoffmann (1948) and referred to these setae as dorsal and ventral humerals. However, these lateral setae are of two distinct morphological types: 1) a humeral seta, and 2) a sternal seta. Because of the position between coxae II and III, the ventralmost humerals will be called lateral humeral setae, and the sternals will be considered lateral sternal setae.

The leg segmentation of this genus should be considered as 7-6-6, with the fusion of the basifemur and telofemur on legs II and III. Most species of *Pseudoschoengastia* were examined, and in some species a definite line of fusion was seen. Loomis (1956:1419) reported that a femoral suture could be discerned in *P. hungerfordi* but seemed to be entirely absent or indistinct in *P. farneri*. The degree of fusion was determined by the thickness and number of heavily sclerotized rings within the femur. When completely fused, there were fewer, less distinct bars. The condition of fusion seemed to be consistent within each species, but varied among different species.

The leg index is the sum of one measured length for each of the legs I, II and III.

*Taxonomic remarks*: *Cordiseta* is another New World genus that shares many characteristics with *Pseudoschoengastia*. These similarities include five branched setae on the palpal tarsus, expanded sensilla, multiple lateral humerals and sternals, and reduced (7-6-6) leg segmentation. The many characteristics shared by *Cordiseta* and *Pseudoschoengastia* indicate a close relationship. They are not closely similar to *Ascoschoengastia, Laurentella,* or other Old World genera.

### Subgenus **Pseudoschoengastia** Lipovsky, 1951

*Referred Species*: Twenty-six species placed into four groups: Hunger-

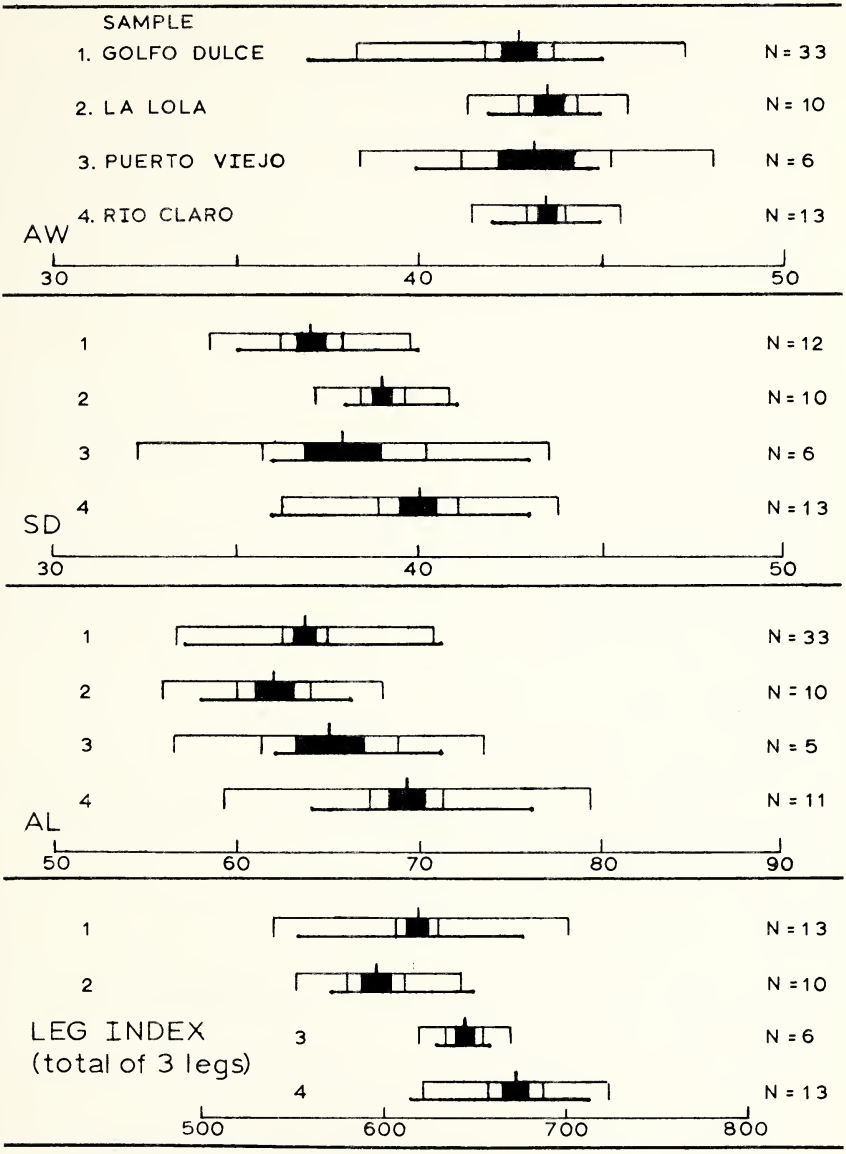



Figure 3. Modified Dice-Leraas diagrams of selected measurements of *Pseudoschoengastia bulbifera* from four different populations: 1. Golfo Dulce Biotic District; 2. Finca "La Lola"; 3. Puerto Viejo de Serapiquí; 4. Río Claro. Measurements, top to bottom, are: AW, anterior width of scutum; SD, scutal depth; AL, length of anterolateral scutal seta; leg index, total length of three legs. N = size of sample.

In each diagram the lower line indicates the total variation of the sample (N); the shaded area one standard error, the adjacent bar twice the standard error on each side of the mean; and the upper line is two standard deviations on each side of the mean.

fordi Group (8 species), Farneri Group (7 species), Anomala Group (8 species), and Aeci Group (3 species).

*Diagnosis*: Larva with posterolateral setae off the scutum; AM<AL>PL, AM=AL<PL or AM>AL<PL; sensilla subcapitate to capitate, setules variable; cheliceral blade with dorsomedial tooth in Hungerfordi and Farneri Groups and without dorsomedial tooth in Anomala and Aeci Groups; galeala nude; eyes 2/2 on a plate or absent; leg segmentation 7-6-6 with fusion of femora II and III; 2 or 3 genualae (solenidia 3) I, genualae ($S_3$) II and III present; tibiala ($S_3$) III present.

*Comments*: This subgenus is represented in Costa Rica by nine species belonging to the four species groups.

### Hungerfordi Group

*Referred species*: *Pseudoschoengastia hungerfordi* Lipovsky, 1951; *P. audyi* Brennan and Jones, 1959; *P. dasypi* Brennan and Yunker, 1966; *P. guatemalensis* Brennan, 1952. In COSTA RICA: *P. bulbifera* Brennan, 1960; *P. intermedia* sp. n.; *P. montana* sp. n.; *P. peromysci* sp. n.

*Diagnosis*: Cheliceral blade with dorsomedial tooth; anterolateral seta longer than other scutal setae; eyes 2/2 on plate; only small setules on postero-ventral surface of sensilla.

*Comments*: This group occurs from Panamá to Kansas in the United States. All four species known from Costa Rica are placed in the Bulbifera Complex.

### Bulbifera Complex

This complex within the Hungerfordi Group includes *Pseudoschoengastia bulbifera* Brennan, *P. intermedia* sp. n., *P. peromysci* sp. n., and *P. montana* sp. n., all from Costa Rica. All have the basal bulb on the stem of the capitate sensilla, and 3 genualae I.

### **Pseudoschoengastia bulbifera** Brennan

Fig. 4

*Pseudoschoengastia bulbifera* Brennan, 1960:483, type from Canal Zone, Panamá, host *Sigmodon hispidus*, 24 Dec. 1954; Brennan and Yunker, 1966:245

*Diagnosis*: Larva, similar to *Pseudoschoengastia audyi* in having 3 genualae I, but differing in having a bulb at base of sensilla and palpal tibial setae BBB (without bulb and setae NNN in *P. audyi*).

*Description* (based on 29 larvae from Costa Rica): Body partially engorged, 189 by 284, color in life probably yellow; eyes 2/2, anterior slightly larger, color in life probably red, ocular plate present.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-4-8-10-8-6 + 20, total 62; dorsal humeral setae 38, 38, lateral humeral seta 32, seta of first posthumeral row 37, posterior dorsal seta measuring 39.

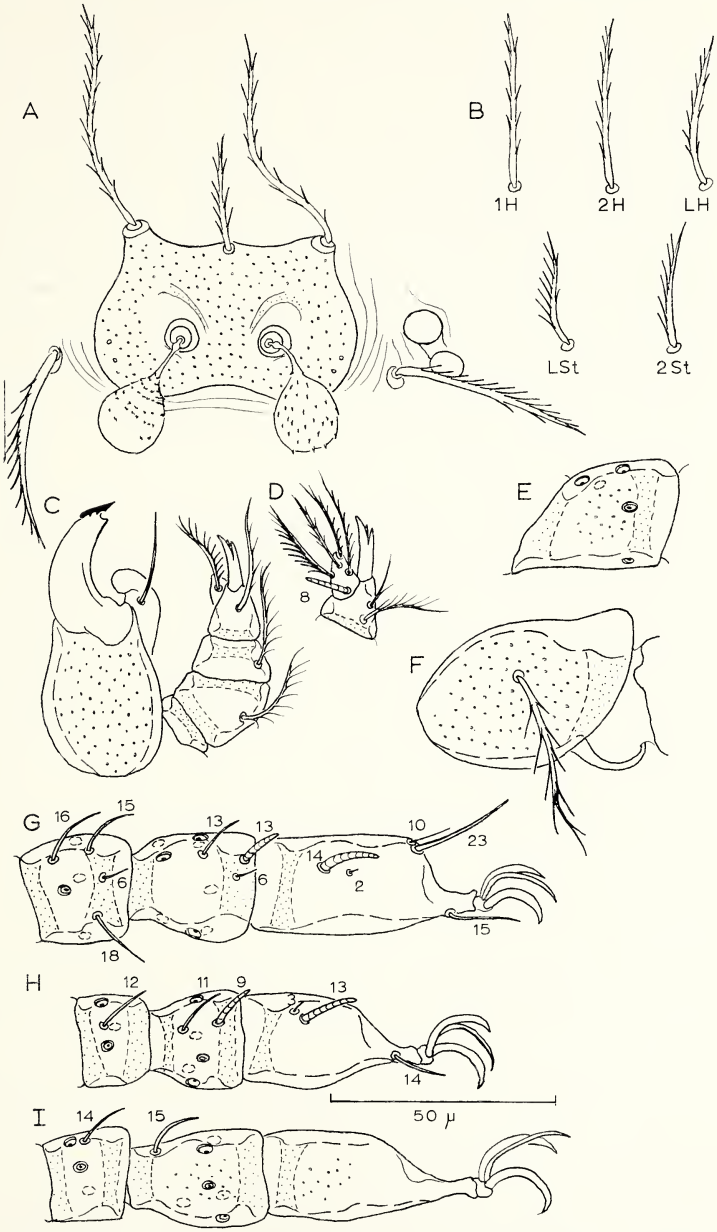



Figure 4. *Pseudoschoengastia bulbifera* Brennan. A. Scutum and eyes. B. Representative body setae: 1H—first dorsal humeral seta; 2H—second dorsal humeral seta; LH—lateral humeral seta; LSt—lateral sternal seta; 2St—second sternal seta. C. Dorsal aspect of gnathosoma showing chelicera, cheliceral base, and palpus. D. Ventral aspect of palpal tibia and tarsus. E. Femur III. F. Coxa III. G. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. H. Leg II; as above. I. Leg III; as above.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-6-6-8-4-2-2, total 34; first, second, and lateral sternal setae 29, 27, 28, posterior ventral seta measuring 21.

Scutum: rectangular with posterolateral margins rounded, posteromedial margin concave. Sensilla subcapitate with two types of setules.

Scutal measurements of 29 specimens (unless otherwise noted) from the Caribbean Costa Rica Biotic District including mean, ±2 SE, and the range (in parentheses): AW, 43 ±1 (40-45); SB, 16 ±1 (13-19); ASB, 26 ±0.5 (24-28); PSB, 14 ±0.5 (11-16); SD, 39 ±1 (36-43); AM, 32 ±2 (26-38, 23); AL, 66 ±2 (58-76, 26); PL, 47 ±1 (44-52); S, 31 ±1 (29-32, 8).

Gnathosoma: cheliceral blade with a tricuspid cap bearing small serrations and a tooth on the dorsomedial surface. Galeala nude.

Leg measurements of above 29 specimens, including mean and the extremes (in parentheses): leg I, 233 (199-256); leg II, 188 (165-213); leg III, 225 (201-253); leg index, 641 (573-713).

Legs: femur of leg III with two internal bars.

*Comments*: Selected measurements of *Pseudoschoengastia bulbifera* are presented from four samples: three from localities within the Caribbean Costa Rica Biotic District, and one from the Golfo Dulce Biotic District. Four of thirteen measurements from each sample are presented in Fig. 3 as modified Dice-Leraas diagrams: 1) anterior width (AW) of scutum, 2) scutal depth (SD), 3) length of anterolateral scutal seta (AL), and 4) the leg index. The variation of each sample broadly overlaps those of all other samples and no significant statistical difference was noted. However, the sample from Río Claro seemed to have slightly longer legs (leg index) and AL setae, than those from the other three areas.

*Ecological notes*: This species is widespread throughout the Caribbean and the Golfo Dulce Biotic Districts in both Tropical and Subtropical Life Zones.

Brennan and Yunker (1966) reported this species from Panamá off one lizard (*Sceloporus*), four species of marsupials (*Didelphis, Marmosa* (2) and *Philander*), one shrew (*Cryptotis*), one monkey (*Saguinas*), one bat (*Sturnira*), and 17 kinds of rodents (*Proechimys, Heteromys* (2), *Liomys, Hoplomys, Sigmodon, Oryzomys* (5), *Peromyscus* (2), *Reithrodontomys, Scotinomys, Zygodontomys* and *Nectomys*).

*Specimens examined*: Total 172 larvae: HEREDIA: Puerto Viejo, 154 m, 14 and 16 Aug. 1963, *Oryzomys caliginosus* (3); 7.5-9.5 km S Puerto Viejo, 15 Aug. 1964, *Oryzomys caliginosus* (2) and *Proechimys semispinosus* (1); El Angel Falls, *Oryzomys albigularis* (=*O. devius*), 6 Feb. 1963 (4); 18 Aug. 1964 (12). CARTAGO: Río Claro, 30 June 1964, *Peromyscus nudipes* (8); Turrialba, 600 m, 22 Sept. 1964, *Oryzomys caliginosus* (7); Tapanti, 1200 m, 3 July 1964, *Peromyscus nudipes* (1). LIMON: finca "La Lola," 23-24 July 1964, *Oryzomys caliginosus* (23). SAN JOSE: 20.8 km N San Isidro del General, 15 July 1963, *Oryzomys albigularis* (=*O. devius*) (9). PUNTA-

RENAS: Río Damitas, 11 Jan. 1963, *Proechimys semispinosus* (1); Río Coronado, 20 km N Puerto Cortez, 7 March 1963, *Proechimys semispinosus* (3); 1.7 km W Palmar Norte, 10 March 1963, *Sigmodon hispidus* (4); 7.3 km S Palmar Sur, 11 Aug. 1963, *Sigmodon hispidus* (9); finca "Los Helechales," 1040 m, 2 Oct. 1964, *Oryzomys alfaroi* (1); and 840 m, 11 Oct. 1964, *Zygodontomys microtinus* (=*Z. cherriei*) (46); 8 km E Potrero Grande, finca de Señor Treno, 660 m, 10 Oct. 1964, *Oryzomys caliginosus* (5); Rincón de Osa, *Oryzomys caliginosus*, 27 June 1963 (3); 3 July 1963 (1), 9-11 July 1964 (10); Camp Seattle, 13 Aug. 1962, *Oryzomys fulvescens* (8); 2.5-6.1 km N Villa Neily, 9-11 Aug. 1963, *Oryzomys fulvescens* (2), *Oryzomys caliginosus* (1), *Proechimys semispinosus* (2), and *Philander opposum* (1). PANAMA: Chiriquí, 31 Jan. and 12 Feb. 1960, *Peromyscus nudipes* (2, RML 35919, 35926).

## **Pseudoschoengastia intermedia** sp. n.

Fig. 5

*Types*: Larvae, holotype and 8 paratopotypes from 20.8 km N San Isidro del General, 1600 m, San José Province, host *Oryzomys albigularis*, field no. 0-2102, collected 15 July 1963 by R. S. Casebeer, H. Coulombe, A. G. Hollister, A. Starrett and C. L. Hogue.

*Diagnosis*: Larva differing from other members of Bulbifera Complex in at least one of the following combinations of characters: teeth on cheliceral cap; palpal setal formula B/B/NNB; 3 internal bars within femur III; and less than 70 dorsal body setae.

*Description of holotype*: Body partially engorged, 143 by 208, color in life yellow; eyes 2/2, anterior larger, ocular plate inconspicuous.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-4-8-10-8-8-8 + 12, total 64; dorsal humeral setae 43, 45, lateral humeral seta 40, seta of first posthumeral row 36, posterior dorsal seta measuring 36.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-10-12-4-2, total 34; first, second and lateral sternal setae 43, 33, 45, posterior ventral seta measuring 17.

Scutum: slightly wider than deep rectangle with posterolateral margins rounded, posteromedial margin concave. Sensilla capitate with few barbs on posterior surface.

Scutal measurements of holotype and (in parentheses) the mean, ± 2 SE, range and total number of specimens measured: AW, 44 (43 ± 1, 40-47, 9); SB, 15 (15 ± 1, 12-19, 9); ASB, 26 (27 ± 1, 26-28, 6); PSB, 15 (14 ± 1, 13-17, 6); SD, 41 (42 ± 1, 41-44, 6); AM, 40 (39 ± 2, 36-43, 8); AL, 76 (74 ± 3, 66-78, 9); PL, 50 (50 ± 1, 45-52, 9); S, 31 (33 ± 1, 31-34, 5).

Gnathosoma: cheliceral blade with small teeth on medial surface of cap. Galeala nude.

Leg measurements of holotype and 5 paratopotypes, including mean and the extremes (in parentheses): leg I, 266 (256-279); leg II, 218 (205-227);

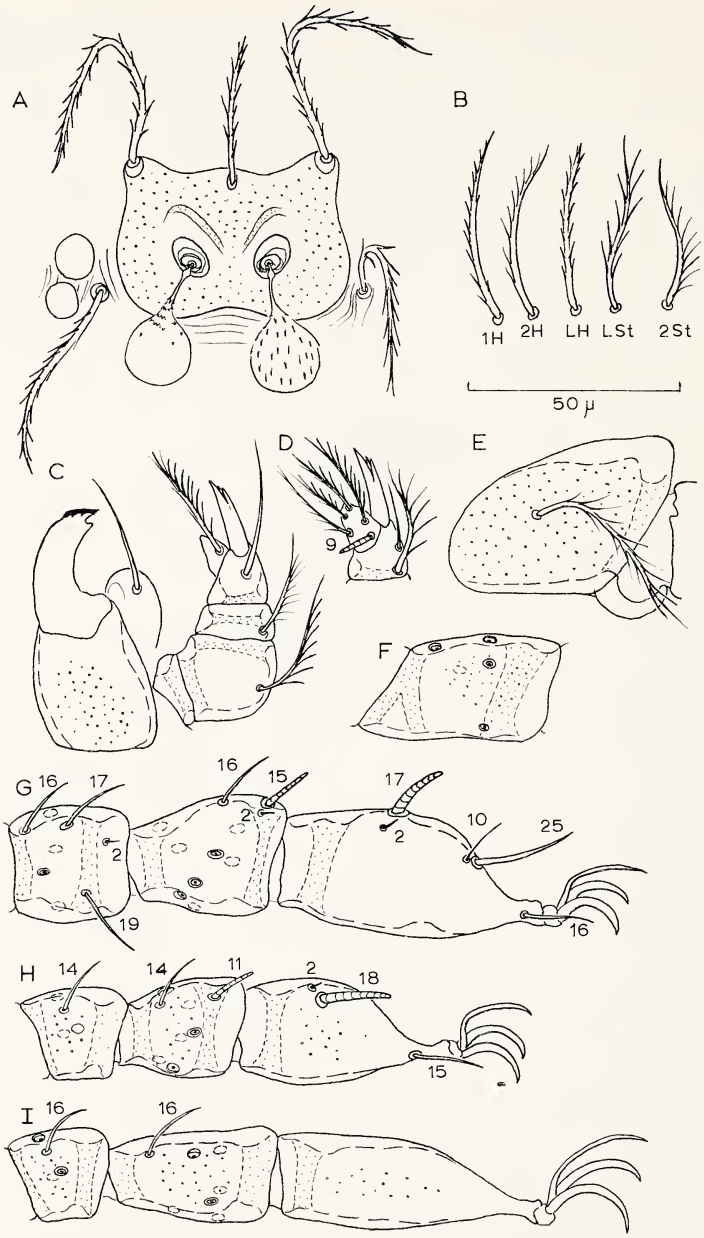



Figure 5. *Pseudoschoengastia intermedia* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Femur III. G. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. H. Leg II. I. Leg III.

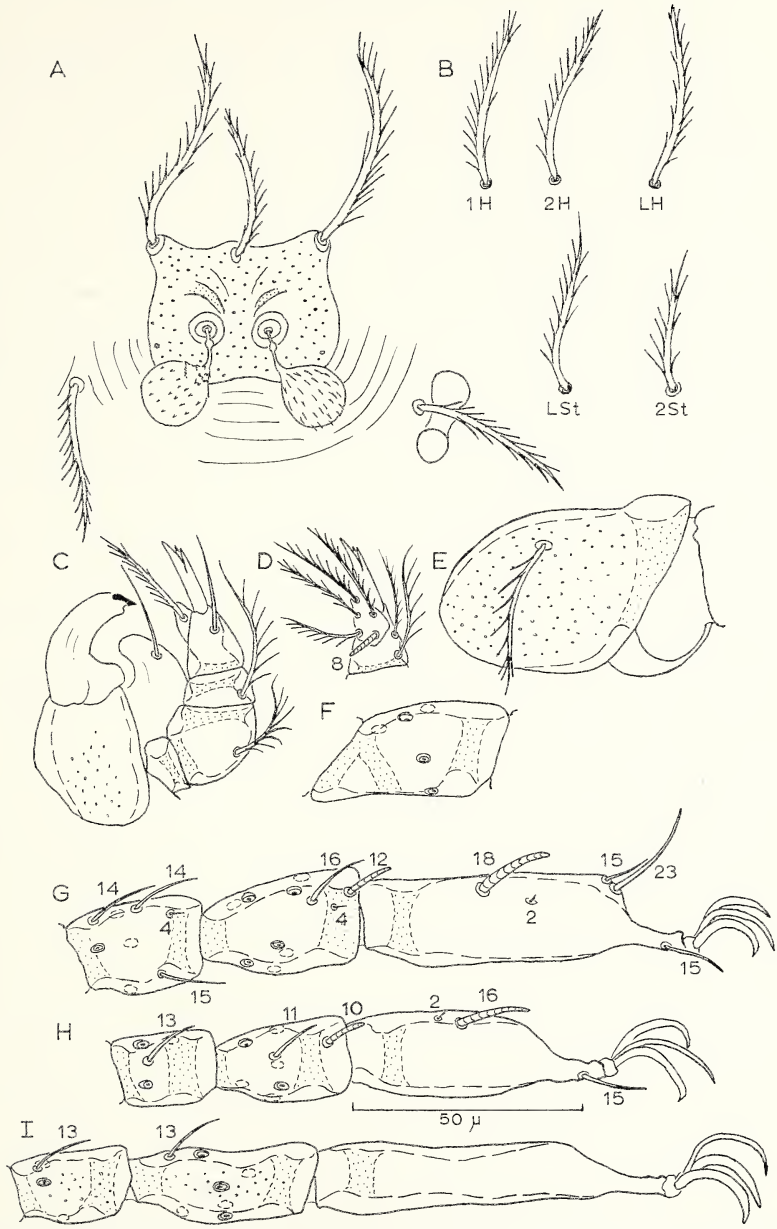



Figure 6. *Pseudoschoengastia montana* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Femur III. G. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. H. Leg II. I. Leg III.

leg III, 262 (237-278); leg index, 749 (709-779).

*Ecological notes*: This species is known only from one locality at the edge of the Panamá Highlands Biotic District. It was found with *Pseudoschoengastia bulbifera* at this locality.

*Specimens examined*: Total of 9 larvae of type series.

## **Pseudoschoengastia montana** sp. n.

Fig. 6

*Types*: Larvae, holotype and 23 paratopotypes: from 11.3 km S La Georgina, 2500 m San José Province, host *Oryzomys albigularis*, holotype and 22 paratypes from field no. 0-2112, taken 16 July 1963 by R. S. Casebeer, H. Coulombe, A. G. Hollister, C. L. Hogue and A. Starrett, 1 paratype (0-1150), taken 20 Nov. 1962 by R. S. Casebeer.

*Diagnosis*: Larva differing from other members of Bulbifera Complex in the following combinations of characters: palpal setal formula B/B/NBB, 3 bars within femur III, and fewer than 70 dorsal body setae.

*Description of holotype*: Body engorged, 284 by 473, color in life probably yellow; eyes 2/2, anterior larger, ocular plate inconspicuous.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-4-8-10-8-6±16, total 58; dorsal humeral setae 38, 38, lateral humeral seta 38, seta of first posthumeral row 28, posterior dorsal seta measuring 37.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-6-6-6-4-2, total 30; first, second and lateral sternal setae 36, 31, 34, posterior ventral seta measuring 22.

Scutum: rectangular with posterolateral margin rounded, sensilla capitate with several rows of barbs on posterior surface.

Scutal measurements of holotype and (in parentheses) the mean, ± 2 SE, range and total number of specimens measured: AW, 32 (35 ± 1, 30-38, 24); SB, 10 (12 ± 1, 9-16, 24); ASB, 22 (24 ± 1, 20-27, 23); PSB, 14 (13 ± 1, 11-16, 22); SD, 36 (36 ± .5, 33-41, 22); AM, 33 (32 ± 1, 28-35, 21); AL, 47 (49 ± 1, 45-52, 22); PL, 37 (35 ± 1, 31-40, 23); S, 26 (25 ± 1, 24-26, 6).

Gnathosoma: cheliceral blade without teeth on cap and with a small tooth on dorsomedial surface. Galeala nude.

Leg measurements of holotype and 23 paratopotypes, including mean and the extremes (in parentheses): leg I, 248 (236-270); leg II, 211 (199-227); leg III, 255 (241-280); leg index, 717 (672-778).

*Ecological notes*: This species is known from three samples: two from the Panamá Highlands Biotic District in the Submontane Life Zone and at the edge of the Subtropical Life Zone in a wet forest formation along a small stream bed; and the third sample of two larvae is from Volcán Poás in the Costa Rica Highlands Biotic District.

*Taxonomic remarks*: The three series of larvae from "Los Helechales,"

south of La Georgina, and Volcán Poás are closely similar in most characteristics. However, it was noted that the legs and tarsalae I and II were shorter in the "Los Helechales" sample. Tarsala I (11-13) and tarsala II (12-14) from "Los Helechales" measured shorter than tarsala I (16-20) and tarsala II (14-16) from La Georgina and Volcán Poás. The leg measurements, means and (in parentheses) the extremes are presented for the "Los Helechales" sample (22 larvae): Leg I, 211 (195-218); leg II, 174 (161-180); leg III, 207 (199-218); leg index, 591 (560-625). Leg measurements of two larvae from Volcán Poás are: Leg I, 238, 235; leg II, 213, 205; leg III, 256, 237; leg index 707, 677.

*Specimens examined*: Total 48 larvae: ALAJUELA: Volcán Poás, 2493 m, 24 March 1963, *Peromyscus nudipes* (2). SAN JOSE: 11.3 km S La Georgina, 2500 m, *Oryzomys albigularis* (=*O. devius*), 20 Nov. 1962 (1), 16 July 1963 (23). PUNTARENAS: Finca "Los Helechales," 15 km E Potrero Grande, 1040 m, 2 Oct. 1964, *Oryzomys alfaroi* (7), *Oryzomys bombycinus* (15).

## **Pseudoschoengastia peromysci** sp. n.

Fig. 7

*Types*: Larvae, holotype and one paratopotype: from Monteverde, 1380 m, Puntarenas Province, host *Peromyscus nudipes*, holotype from field no. 0-2831, obtained 14 May 1964 by C. A. McLaughlin, F. S. Truxal and J. M. Savage; and paratopotype from 0-2809-10, taken 13 May 1964 by same collectors.

*Diagnosis*: Larva differing from other members of Bulbifera Complex in having a palpal setal formula of B/B/NNB; ASB, 30-32 (24-28 in *P. bulbifera*); 3 bars within fused femur III; more than 80 dorsal body setae; legs long; and scutum small.

*Description of holotype*: Body unengorged, 151 by 246, color in life yellow; eyes 2/2, equal, ocular plate present, color in life probably red.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-4-6-10-8-6 + 50, total 90; dorsal humeral setae 49, 52, lateral humeral seta 50, seta of first posthumeral row 43, posterior dorsal seta measuring 43.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-8-10-8 + 6, total 38; first absent, second and lateral sternal setae 47, 57, posterior ventral seta measuring 26.

Scutum: rectangular, as deep as wide with posterolateral margins rounded, posteromedial margin concave, sensilla capitate with 2 types of setules.

Scutal measurements of holotype and single paratopotype (in parentheses): AW, 36 (38); SB, 14 (14); ASB, 30 (32); PSB, 16 (16); SD, 36 (38); AM, 47 (42); AL, 76 (79); PL, 57 (52); S, 31.

Gnathosoma: cheliceral blade with tricuspid cap and small tooth on the dorsomedial surface. Galeala nude.

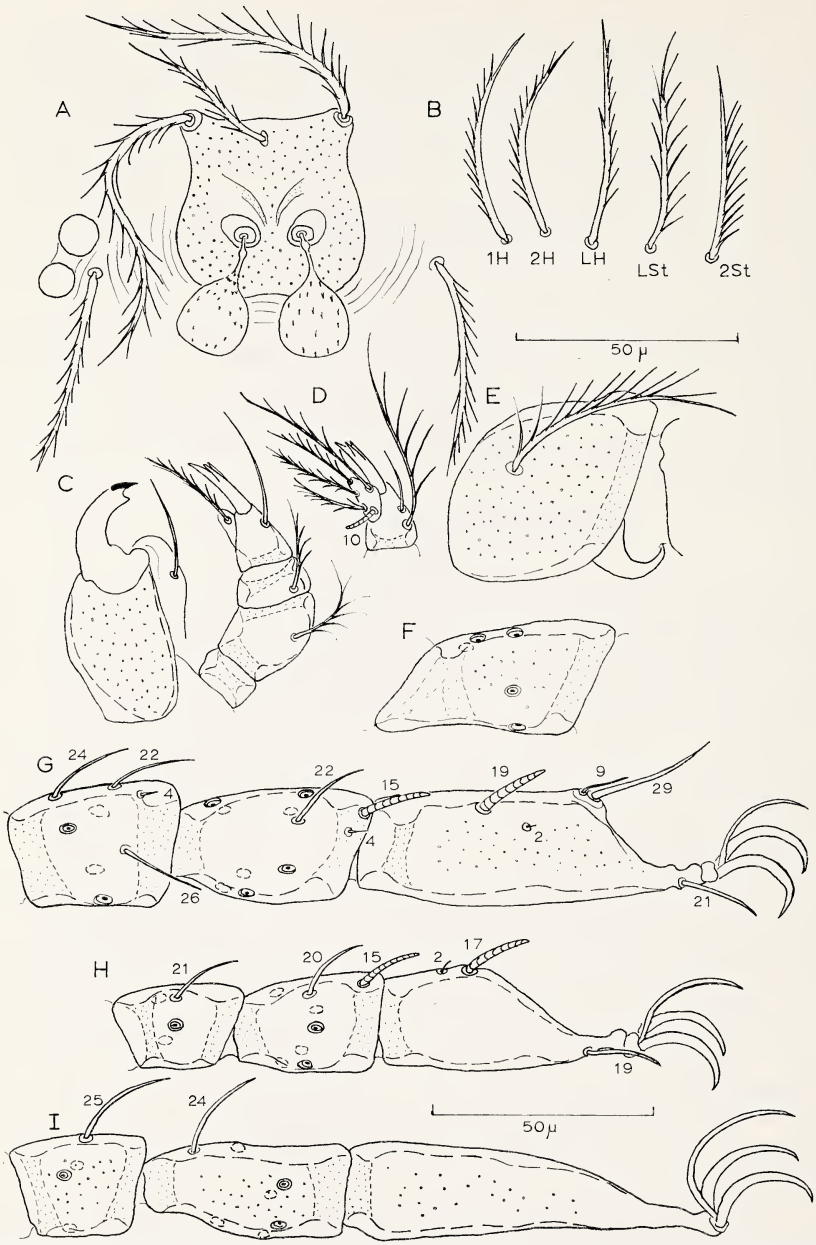



Figure 7. *Pseudoschoengastia peromysci* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Femur III. G. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. H. Leg II. I. Leg III.

Leg measurements of holotype and paratopotype: leg I, 360, 350; leg II, 289, 284; leg III, 341, 322; leg index, 990, 956.

*Ecological notes*: This species, as well as *P. bulbifera* and *P. zona,* was taken off a series of *Peromyscus nudipes* from the Costa Rica Highlands Biotic District.

*Taxonomic remarks*: *P. peromysci* has the longest legs and the smallest scutum of any species in the Bulbifera Complex.

*Specimens examined*: Total of 2 larvae of type series.

Farneri Group

*Referred species*: *Pseudoschoengastia farneri* Lipovsky, 1951; *P. hypopsia* Brennan and Jones, 1959; *P. scitula* Brennan and Jones, 1959. In COSTA RICA: *P. hoguei* sp. n.; *P. hooperi* sp. n.; *P. rheomys* sp. n.; and *P. zona* Brennan, 1960.

*Diagnosis*: Palpal femoral seta shorter than nude genual seta; cheliceral blade with tricuspid cap (no teeth) and a dorsomedial tooth; AL<AM<PL or AM<AL <PL; eyes 2/2 on a plate; 2 pairs of dorsal humerals and 1 pair of lateral humerals; 1 pair of lateral sternal setae.

*Comments*: This group occurs from Kansas to Panamá. Three new species of the group are described from Costa Rica. In Costa Rica and Panamá, members of this group have few or no branches on the palpal setae, and the palpal femoral seta is branched only in *Pseudoschoengastia zona* and *P. hoguei* sp. n. This characteristic also obtains for *P. abditiva* of the Anomala Group.

**Pseudoschoengastia zona** Brennan

Fig. 8

*Pseudoschoengastia zona* Brennan, 1960:490, type from Canal Zone, Curundu, Panamá, host *Liomys adspersus,* 8 July 1954; Brennan and Yunker, 1966:248.

*Diagnosis*: Larva similar to *Pseudoschoengastia scitula* of southern México in having palpal setal formula of B/N/NNN, but differing from it in having AM seta shorter than AL seta.

*Description* (4 referred specimens from Panama and 7 larvae from Costa Rica): Body partially engorged, 133 by 189, color in life probably red, ocular plate present.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-6-10-12-12-12-8-6 + 14, total 86; dorsal humeral setae 29, 29, lateral humeral seta 30, seta of first posthumeral row 22, posterior dorsal seta measuring 26.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-8-10-8-4-4-2, total 36; first, second and lateral sternal setae 30, 24, 27, posterior ventral setae measuring 19.

Scutum: Rectangular with rear margin concave, sensilla capitate with setules of two types.

Scutal measurements including mean and range of 2 paratypes and 2

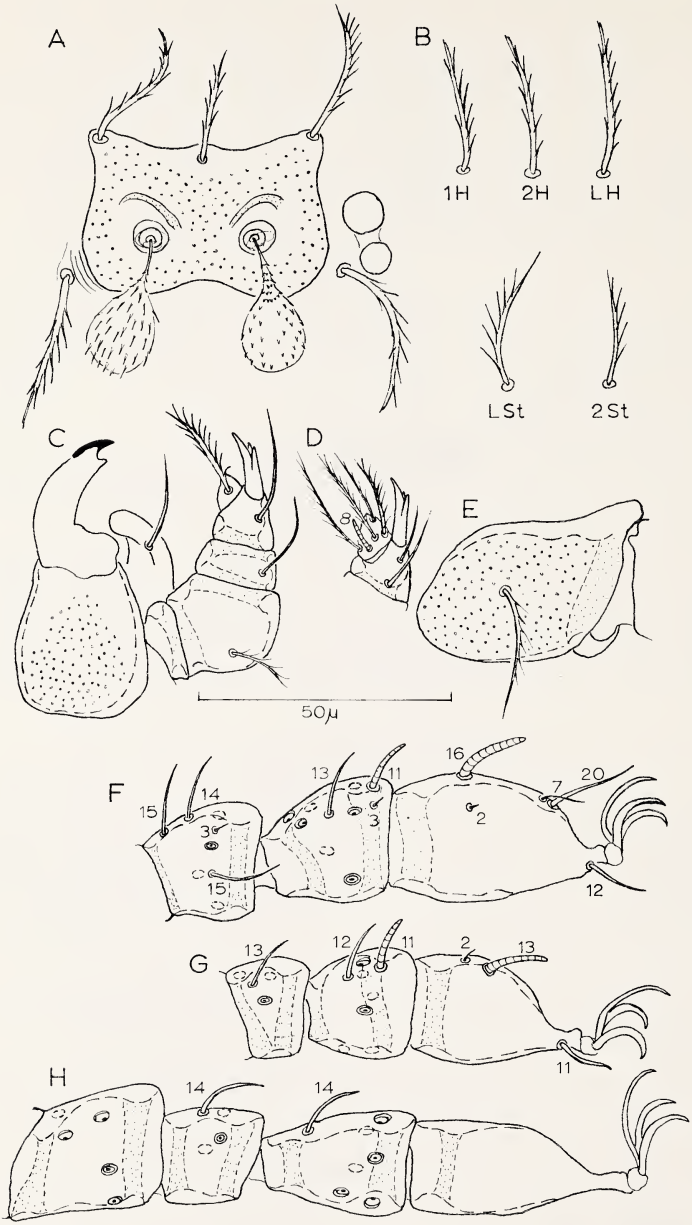



Figure 8. *Pseudoschoengastia zona* Brennan. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

referred specimens from Panamá and (in parentheses) the mean ± 2 SE, and the range of 7 specimens from Costa Rica: AW, 52, 47-56 (46 ± 1, 44-47); SB, 28, 26-30 (24 ± 2, 21-27); ASB, 23, 21-25 (23 ± 1, 21-25); PSB, 16, 14-18 (13 ± 2, 11-16); SD, 39, 35-42 (36 ± 1, 34-38); AM, 27, 24-30 (25 ± 1, 24-26); AL, 28, 27-30 (28 ± 3, 23-35); PL, 37, 35-38 (35 ± 2, 32-38); S, 30, 30-31 (30 ± 1, 28-32).

Gnathosoma: cheliceral blade with a tricuspid cap and dorsomedial tooth. Galeala nude.

Leg measurements of 2 paratypes and 2 referred specimens from Panamá, including means and extremes and (in parentheses) 7 specimens from Costa Rica: leg I, 203, 189-215 (200, 184-218); leg II, 168, 165-170 (160, 151-170); leg III, 204, 194-213 (197, 184-213); leg index, 569, 543-589 (557, 519-601).

*Ecological notes*: The range of this species extends from Golfo Dulce Biotic District to lower elevations of the Panamá-Costa Rica Highlands Biotic Province but it was not taken in the Guanacaste and Caribbean Costa Rica Biotic Districts. In Costa Rica it was taken from *Oryzomys, Zygodontomys, Proechimys* and *Peromyscus,* all of which are new host records. In Panamá it was obtained from five genera, *Heteromys, Liomys, Oryzomys, Sigmodon,* and *Tylomys* (Brennan and Yunker, 1966.)

*Specimens examined*: Total 11 larvae: SAN JOSE: 20.8 km N San Isidro del General, 15 July 1963, *Oryzomys albigularis* (=*O. devius*) (3). PUNTARENAS: Monteverde, 1380 m, 13 May 1964, *Peromyscus nudipes* (2); 12 km E Potrero Grande, finca "Los Helechales," 1040 m, 11 Oct. 1964, *Zygodontomys microtinus* (=*Z. cherriei*) (1); Rincón de Osa, 14 July 1964, *Proechimys semispinosus* (1). PANAMA: Canal Zone, National Forest, 20 April 1955, *Sigmodon hispidus* (paratype, RML 35239); Canal Zone, Summit Gardens, 21 Sept. 1954, *Liomys adspersus* (RML 35267, paratype); Canal Zone, Nuevo Emperador, 7 Aug. 1961, *Liomys adspersus* (2, RML 43336, 43338).

## **Pseudoschoengastia hoguei** sp. n.

Fig. 9

*Types*: Larvae, holotype and 53 paratypes: holotype and 40 paratopotypes from 7.5 km S Liberia, Guanacaste Province, host *Liomys salvini,* field no. 0-3290, taken 8 Aug. 1964 by C. L. Hogue, R. C. Stephens and J. C. Geest; 8 paratypes, 5 km NW Tilarán, *Liomys salvini* (0-438), 28 July 1962 by F. S. Truxal, C. A. McLaughlin, R. S. Casebeer, A. A. Schoenherr; and 5 paratypes, 3 km S Playa del Coco, *Liomys salvini* (0-328 to 339), 23 July 1962, same collectors.

*Diagnosis*: Larva resembling *Pseudoschoengastia zona* and *P. abditiva* in having palpal setal formula of B/N/NNN, but differing from them in having 2 (rather than 3) genualae I and tarsalae I and II being subequal (tarsala I longer than II in *P. zona*), and in having shorter scutal and body setae.

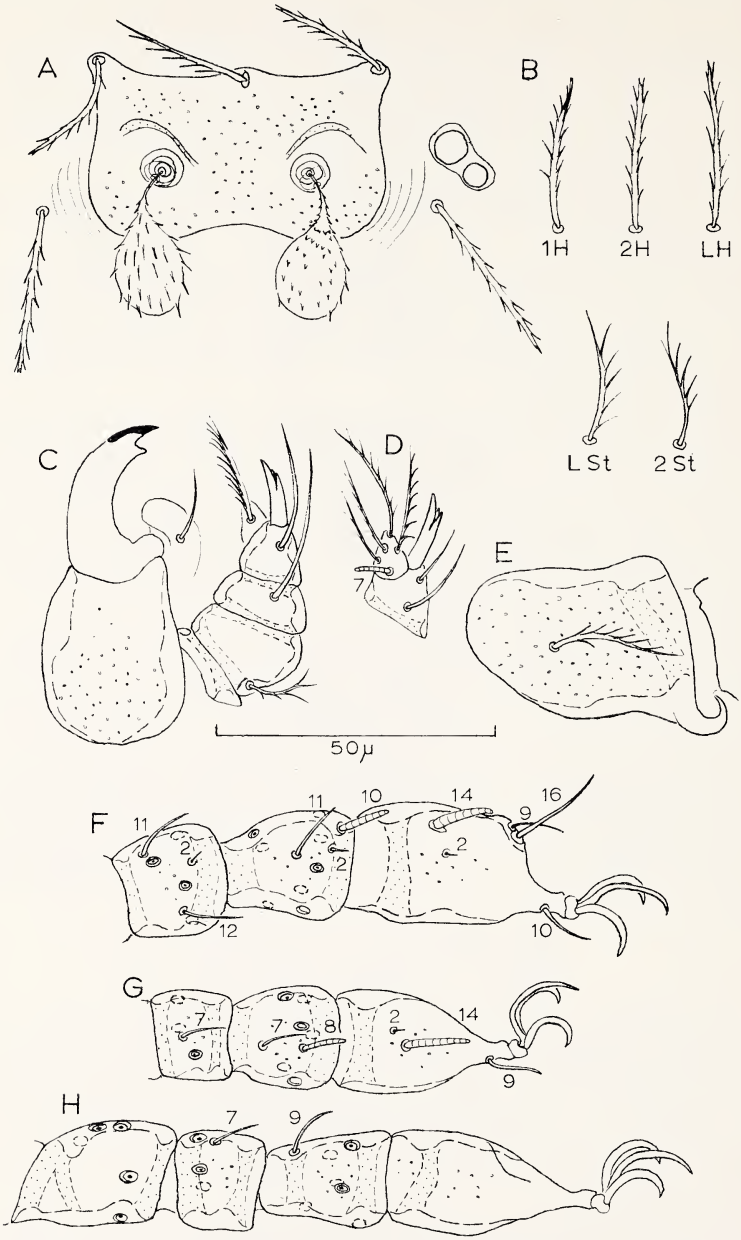



Figure 9. *Pseudoschoengastia hoguei* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

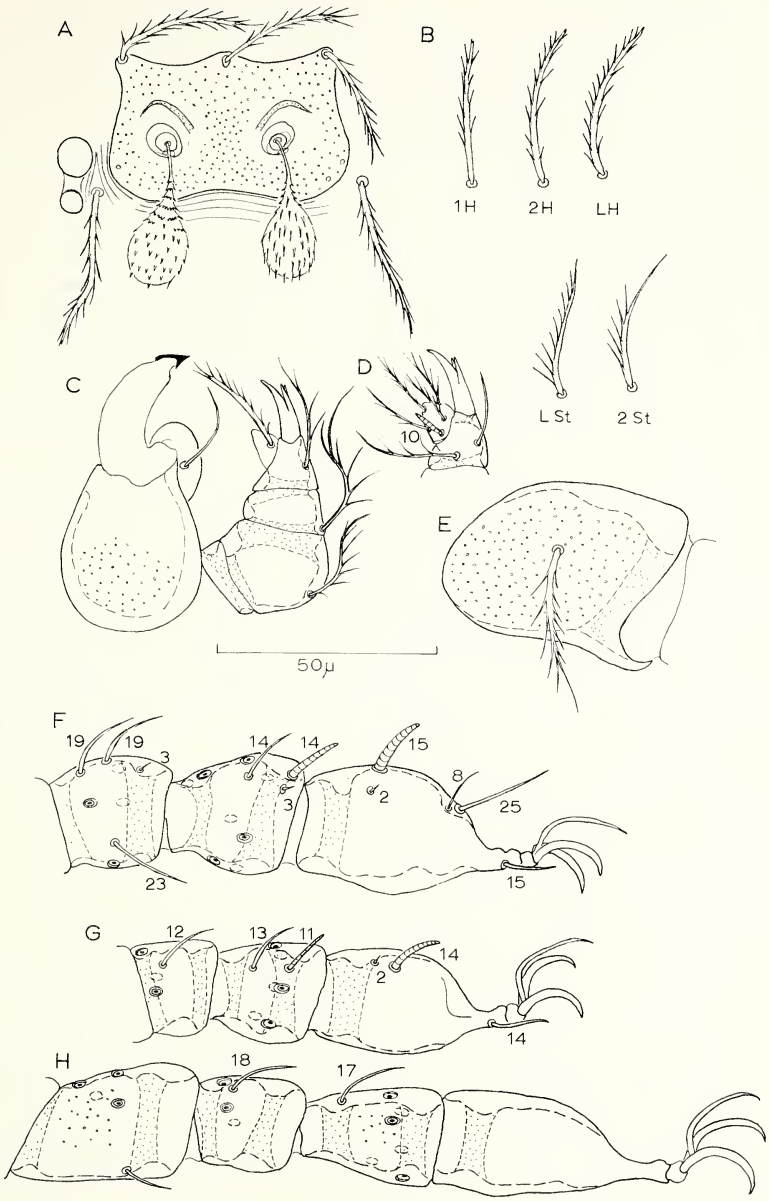



Figure 10. *Pseudoschoengastia rheomys* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

*Description of holotype*: Body engorged, 284 by 199, color in life yellow; eyes 2/2, anterior larger, ocular plate present, color in life probably red.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-4-12-6-12-6-12-6, total 64; dorsal humeral setae 29, 28, lateral humeral seta 30, seta of first posthumeral row 20, posterior dorsal seta measuring 22.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-8-9-8 + 26, total 57; first, second and lateral sternal setae 22, 21, 25, posterior ventral seta measuring 17.

Scutum: rectangular with rear margin concave, sensilla clavate with many barbules.

Scutal measurements of holotype and (in parentheses) the mean, ± 2 SE, and range of holotype and 20 paratypes, unless otherwise noted: AW, 48 (49 ± 1, 46-52, 20); SB, 27 (26 ± 1, 22-27); ASB, 22 (21 ± 1, 20-24); PSB, 14 (12 ± 1, 10-16); SD, 36 (34 ± 1, 30-37); AM, 21 (23 ± 1, 19-27, 19); AL, 25 (24 ± 1, 21-26, 20); PL, 30 (31 ± 1, 27-35); S, 29 (29 ± 1, 27-32, 11).

Gnathosoma: cheliceral blade with tricuspid cap and a deeply emarginate tooth on dorsomedial surface. Palpal setal formula B/N/NNN. Galeala nude.

Leg measurements of holotype and (in parentheses) mean and extremes of holotype and 19 paratypes: leg I, 180 (175, 156-189); leg II, 133 (139, 123-152); leg III, 161 (167, 156-183); leg index, 474 (477, 440-520).

*Ecological notes*: This species was recovered only from *Liomys salvini* captured in the dry forest formation of the Guanacaste Biotic District. Unlike the similar *Pseudoschoengastia zona, P. hoguei* seems to have a narrow host preference. All larvae were taken in July and August at the start of the rainy season.

*Specimens examined*: Total of 137 larvae: GUANACASTE (all off *Liomys salvini*); 3 km S Playa del Coco, 23 July 1963 (5); 5 km NW Tilarán, 28 July 1962 (8); 7.5 km S Liberia, 8 Aug. 1964 (124).

### **Pseudoschoengastia rheomys** sp. n.

Fig. 10

*Types*: Larvae, holotype and 55 paratypes: holotype and 9 paratopotypes from 18 km N San Isidro del General, 1580 m, San José Province, host *Rheomys hartmanni,* field no. 0-2098, taken 14 July 1963 by R. S. Casebeer, H. Coulombe, A. G. Hollister, C. L. Hogue and A. Starrett; and 46 paratypes from 15 km N San Isidro del General, 1495 m, *Rheomys hartmanni,* 21 July 1962 by E. T. Hooper, *et al.*

*Diagnosis*: Larva resembling *Pseudoschoengastia zona* in having short palpal femoral seta, and densely punctate scutum, but differing in having palpal genual and tibial setae branched.

*Description of holotype*: Body partially engorged, 265 by 180, color in life yellow; eyes 2/2, anterior larger, ocular plate present, color in life probably red.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-4-10-10-8-8-8-6, total 60; dorsal humeral setae 40, 36, lateral humeral seta 37, seta of first posthumeral row 31, posterior dorsal seta measuring 35.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-6-6 ± 14, total 32; first, second and lateral sternal setae 38, 32, 36, posterior ventral seta measuring 21.

Scutum: rectangular with rear margin concave, sensilla clavate with barbules of two types.

Scutal measurements of holotype and (in parentheses) the mean, ± 2 SE, and range of 21 specimens unless otherwise noted: AW, 49 (47 ± 1, 43-52); SB, 27 (27 ± 1, 24-31, 19); ASB, 24 (24 ± 1, 22-27, 20); PSB, 15 (14 ± 1, 12-17); AM, 34 (36, ± 2, 29-39, 14); AL, 42 (38 ± 2, 30-44, 16); PL, 41 (42 ± 1, 39-45); S, 33 (33 ± 3, 30-35, 7).

Gnathosoma: cheliceral blade with tricuspid cap and small tooth on dorsomedial surface. Palpal setal formula B/B/BNB. Galeala nude.

Leg measurements of holotype and paratypes, including means, extremes and (in parentheses) the number of specimens: leg I, 259, 246-272 (7); leg II, 209, 199-218 (8); leg III, 265, 256-279 (7); leg index, 728, 701-749 (5).

*Ecological notes*: This chigger is known from the Panamá Highlands Biotic District. The host, a water mouse of the genus *Rheomys,* inhabits small jungle streams and the hind feet are fimbriated and slightly webbed, suggesting that it may spend a good deal of time in the water (Hall and Kelson, 1959). These chiggers were taken from deep within the external auditory meatus of the ears of all six *Rheomys hartmanni* examined. Examination of three *Oryzomys,* three *Peromyscus,* and a *Scotinomys* trapped in the same area failed to reveal this species.

*Specimens examined*: Total of 56 larvae of type series.

## **Pseudoschoengastia hooperi** sp. n.

Fig. 11

*Types*: Larvae, holotype and 9 paratypes from Río Poasito, Volcán Poás Highway, 2000 m, Alajuela Province, host *Rheomys underwoodi,* 7 April 1966 from field numbers JHB 447 and 448 and 0-3751, taken by J. H. Brown and A. Starrett.

*Diagnosis*: Larva resembling *Pseudoschoengastia zona* and *P. rheomys* in having a short palpal femoral seta, and similar densely punctate scutum, but differing from *P. zona* in having palpal genual seta branched and from *P. rheomys* in having all three palpal tibial setae nude.

*Description of holotype*: Body partially engorged, 180 by 265; color in preservative yellow; eyes 2/2, anterior larger, ocular plate present, color probably red.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-8-8-9-8-8-14-14+66, total 143; dorsal humeral setae 55, 49, lateral humeral seta 45, seta of first posthumeral row 31, posterior dorsal seta measuring 47.

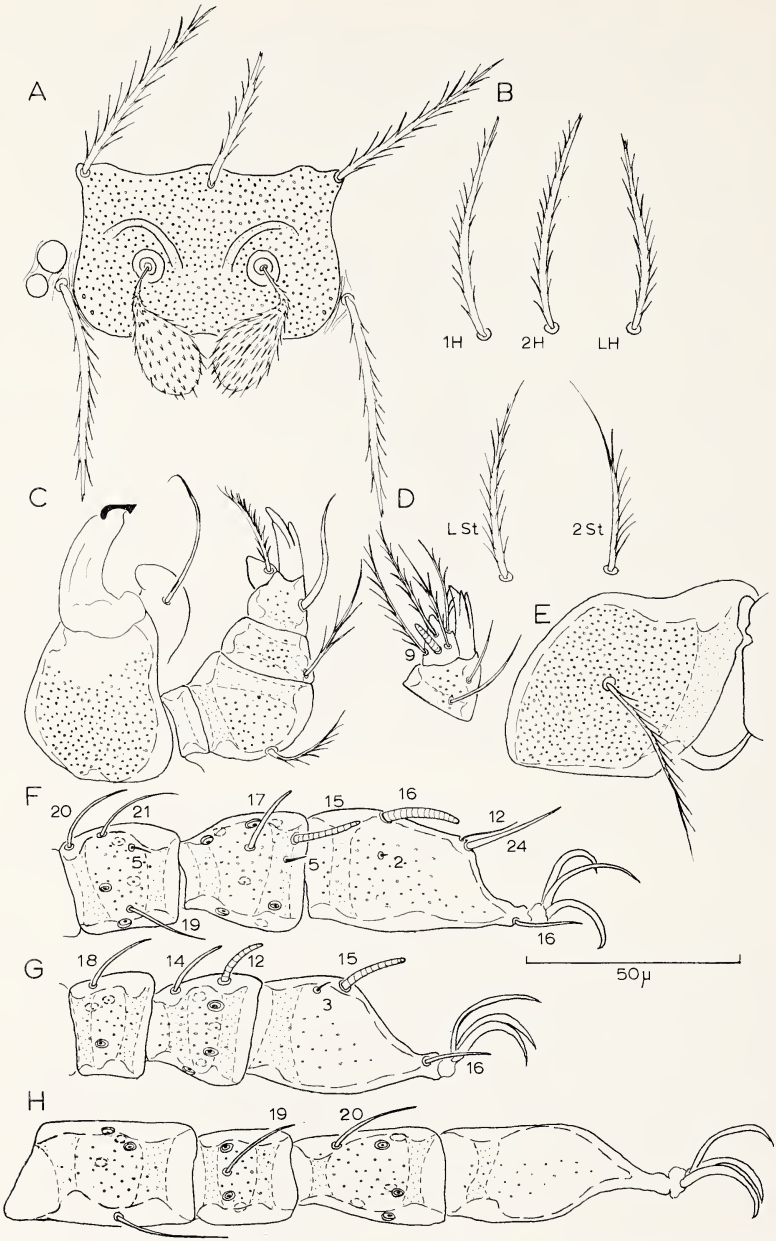



Figure 11. *Pseudoschoengastia hooperi* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

Ventral setal formula 2-2 (sternals)-2 (laterals sternals)-10-10-6+4, total 30; first, second and lateral sternal setae 43, 32, 38, posterior ventral seta measuring 25.

Scutum: rectangular with rear margin slightly concave, sensilla clavate with barbules of two types.

Scutal measurements of holotype and (in parentheses) the mean, ± 2 SE, and range of 10 in type series unless otherwise noted: AW, 56 (56 ± 2, 52-61); SB, 25 (27 ± 2, 23-29); ASB, 27 (27 ± 1, 26-30); PSB, 16 (16 ± 1, 15-17); AM, 45 (45, ± 1, 44-46, 3); AL 49 (47 ± 2, 44-49, 6); PL, 57 (54 ± 2, 47-59); S, 36 (36 ± 1, 35-37, 7).

Gnathosoma: cheliceral blade with tricuspid cap and small dorsomedial tooth. Palpal setal formula B/B/NNN. Galeala nude.

Leg measurements of holotype and paratopotypes, including mean and extremes, and (in parentheses) the number of specimens: leg I, 237, 246, 237-251, (9); leg II, 204, 203, 199-210 (7); leg III, 251, 268, 251-279 (5); leg index 720, 718, 692-737 (5).

*Remarks*: *Pseudoschoengastia hooperi* resembles and seems to be closely related to *P. rheomys,* also recovered from water mice of the genus *Rheomys.* The species *P. hooperi* is known only from the type locality in the Costa Rica Highlands Biotic District.

*Specimens examined*: Total of 10 larvae of type series.

Anomala Group

*Referred species*: *Pseudoschoengastia anomala* (Hoffmann, 1951); *P. brennani* Hoffmann, 1960; *P. diazi* (Hoffmann, 1948); *P. extrinseca* Brennan, 1960; *P. occidentalis* Brennan, 1957; *P. pedregalensis* (Hoffmann, 1951); *P. tricosa* (Brennan and Jones, 1961). In COSTA RICA: *P. abditiva* Brennan, 1960.

*Diagnosis*: Species having palpal setae of approximately equal lengths, cheliceral blade with small tricuspid cap and without dorsomedial tooth, AL < AM < PL, sensilla expanded to subcapitate with setules of one length, eyes 2/2 on a plate, 1-2 pairs of dorsal humerals, 1 pair of lateral humerals, 1-3 pairs of lateral sternal setae (except *P. tricosa*); leg segmentation 7-6-6 but with line of articulation usually visible.

*Comments*: This group of species ranges from California (*P. occidentalis*) to Panamá (*P. tricosa*). *Pseudoschoengastia tricosa* and *P. abditiva* closely resemble each other in most characteristics. *Pseudoschoengastia abditiva* is the only species of this group known from Costa Rica.

**Pseudoschoengastia abditiva** Brennan

Fig. 12

*Pseudoschoengastia abditiva* Brennan, 1960: 482, type from Cerro Azul, Panamá, host *Oryzomys capito,* 8 Feb. 1956.

*Diagnosis*: Larva similar to *Pseudoschoengastia zona* in having a palpal

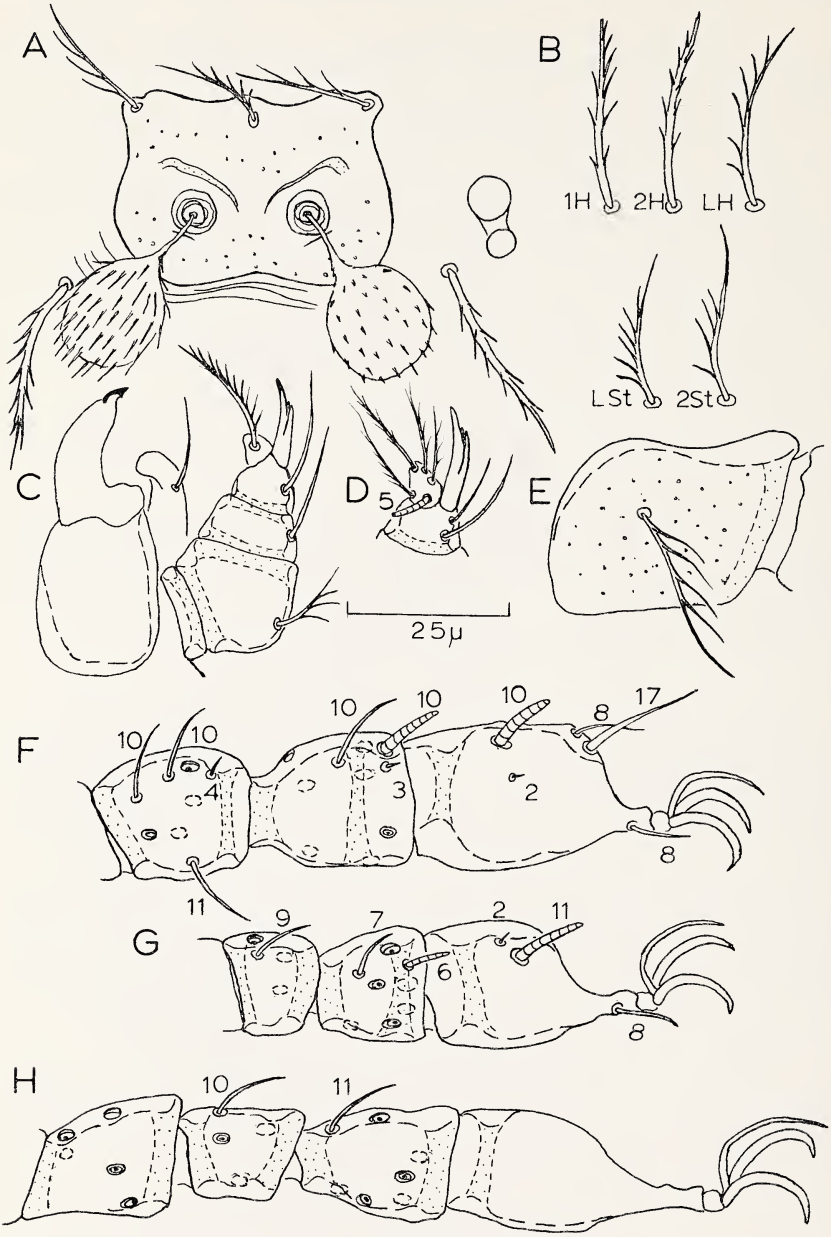



Figure 12. *Pseudoschoengastia abditiva* Brennan. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg. II. H. Leg III; fused femur with internal bars.

setal formula of B/N/NNN, but differing from it in having narrow SB, 13-18 (21-30 in *P. zona*), and lacking dorsomedial tooth on cheliceral blade.

*Description* (paratype and 14 larvae from Costa Rica): Body partially engorged, 180 by 256, color in life probably yellow; eyes 2/2, anterior larger, color in life probably red, ocular plate present.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-6-10-10-10-8-4-2 + 12, total 68; dorsal humeral setae 29, 27, lateral humeral seta 26, seta of first posthumeral row 21, posterior dorsal seta measuring 24.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-8-4-4-4-2-2, total 30; first, second and lateral sternal setae 31, 25, 21 and posterior ventral seta measuring 16.

Scutum: roughly square with rear margin concave, sensilla capitate with two types of setules.

Scutal measurements of one paratype from Panamá and (in parentheses) the mean, ± 2 SE and range of 14 specimens, unless otherwise noted: AW, 33 (31 ± 1, 29-34); SB, 18 (15 ± 1, 13-17); ASB, 19 (19 ± 1, 17-21); PSB, 17 (11 ± 1, 9-12); SD, 36 (29 ± 1, 27-32); AM, 24, (20 ± 1, 19-24, 12); AL, 22 (22 ± 1, 19-23); PL, 32, (31 ± 1, 29-33); S, 27 (28 ± 1, 26-29, 7).

Gnathosoma: cheliceral blade with tricuspid cap; cheliceral base and capitular sternum sparsely punctate. Palpal setal formula B/N/NNN; palpotibial claw with 3 prongs deeply cleft. Galeala nude.

Leg measurements of paratype and (in parentheses) means and extremes of 14 specimens from Costa Rica: leg I, 170 (163, 156-170); leg II, 147 (133, 128-139); leg III, 170 (159, 149-168); leg index, 487 (453, 436-477).

*Specimens examined*: Total of 16 larvae; PUNTARENAS: 15 km E Potrero Grande, finca "Los Helechales," 1040 m, 2 Oct. 1964, *Oryzomys alfaroi* (5), *Oryzomys bombycinus* (10). PANAMA: Cerro Azul, 8 Feb. 1956, *Oryzomys capito* (= *O. talamancae*) (paratype, RML 35338).

### Aeci Group

*Referred species*: *Pseudoschoengastia aeci* Brennan, 1965, and *P. myoproctae* Fauran, 1960. In COSTA RICA: *P. finitima* Brennan and Yunker, 1966.

*Diagnosis*: Species having cheliceral blade with large elongate tricuspid cap and without dorsomedial tooth; AL<AM<PL; scutum only moderately punctate (densely punctate in other groups); eyes 2/2 on a plate, or absent.

### **Pseudoschoengastia finitima** Brennan and Yunker

Fig. 13

*Pseudoschoengastia finitima* Brennan and Yunker, 1966: 246, type from Piña, Canal Zone, Panamá, host *Heteromys desmarestianus*, 7 Dec. 1960.

*Diagnosis*: Larva similar to *Pseudoschoengastia hypopsia*, *P. myoproctae* and *P. aeci* in having 2 genualae I, but differing from *P. hypopsia* and *P. myo-*

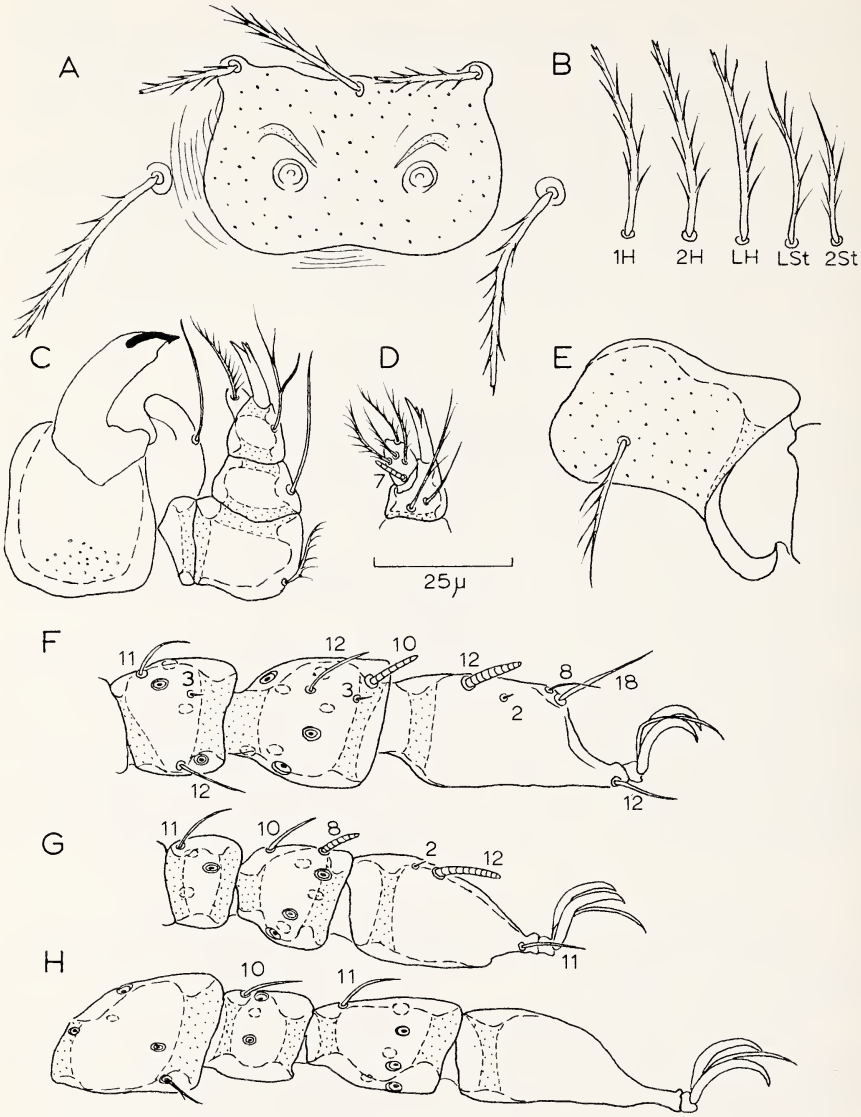



Figure 13. *Pseudoschoengastia finitima* Brennan and Yunker. A. Scutum. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

*proctae* in having genualae II and III, and from *P. aeci* by lacking eyes (eyes 2/2 on a plate in *P. aeci*).

*Description*: (2 paratypes from Panamá and 6 larvae from Costa Rica). Body partially engorged, 189 by 360, color in life probably yellow; no eyes.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-6-8-10-2 + 30, total 62; dorsal humeral setae 34, 33, lateral humeral seta 32, seta of first posthumeral row 25, posterior dorsal seta measuring 27.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-10-8-8-4-2-2, total 40; first, second and lateral sternal setae 27, 24, 26, posterior ventral seta measuring 24.

Scutum: rectangular with rear margin concave.

Scutal measurements of holotype (Brennan and Yunker, 1966), 2 paratypes and (in parentheses) the mean, ± 2 SE and range of 6 specimens from Costa Rica: AW, 47, 45, 45 (42 ± 1, 40-43); SB, 25, 27, 27 (22 ± 1, 20-23); ASB, 21, 21, 23 (21 ± 1, 19-22); PSB, 10, 12, 12 (13 ± 1, 12-15); SD, 31, 33, 35 (34 ± 2, 31-37); AM, 33, 33, 33 (32 ± 1, 31-33, 4); AL, 24, 25, 27 (19 ± 1, 18-20); PL, 42, 43, 43 (38 ± 1, 37-40). Sensilla unknown.

Gnathosoma: cheliceral blade with a tricuspid cap and long ventromedial projection. Cheliceral base and capitular sternum sparsely punctate. Palpal setal formula B/N/BNB. Galeala nude.

Leg measurements of 2 paratypes and the means and extremes of 6 specimens from Costa Rica (in parentheses): leg I, 208, 213, (185, 170-204); leg II, 180, 183 (158, 150-170); leg III, 203, 199 (172, 161-184); leg index, 591, 595, (513, 481-543).

*Specimens examined*: Total of 8 larvae: HEREDIA: 2.9 km S Puerto Viejo de Serapiquí, 89 m, 17 Aug. 1964, *Heteromys desmarestianus* (6); PANAMA, Canal Zone, Piña, 7 Dec. 1960, *Heteromys desmarestianus* (RML 40112, 2 paratypes).

### Subgenus **Walchioides** Vercammen-Grandjean, 1960

*Type species*: *Walchia gouldi* Hoffmann, 1954.

*Referred species*: Ten species: *Pseudoschoengastia gouldi* (Hoffmann), *P. hoffmannae* Brennan, 1960; *P. intrinseca* Brennan, 1960; *P. inevicta* Brennan, 1960; *P. whartoni* Brennan, 1960; *P. apista* Brennan and Yunker, 1966; and *P. mermeriza* Brennan and Yunker, 1966. In COSTA RICA: *P. guanacastensis* sp. n.; *P. costaricensis* sp. n.; and *P. verdensis* sp. n.

*Diagnosis*: Larva with posterolateral setae on scutum; AM>AL<PL; sensilla clavate to subcapitate, all setules prominent; cheliceral blade without dorsomedial tooth; eyes 2/2 on a plate; leg segmentation 7-6-6 but with line of articulation usually visible; 1 or 2 genualae I, genualae II and III present or absent, tibiala III present.

*Taxonomic remarks*: Originally *Walchioides* was proposed by Vercammen-Grandjean (1960) as a subgenus of *Susa*, a genus of southeast Asia, to which it does not belong. Although the type species, *Walchia gouldi* Hoff-

mann, from Chiapas, México, lacks the AM scutal seta, it resembles the other species of *Walchioides* in virtually all of the other characteristics.

*Comments*: This subgenus is represented in Costa Rica by three new species, two from the Guanacaste Biotic District and one from the adjacent Costa Rica Highlands Biotic District.

### **Pseudoschoengastia guanacastensis** sp. n.

Fig. 14

*Types*: Larvae, holotype and 12 paratypes: holotype and 2 paratopotypes from 8.3 km N Liberia, 144 m, Guanacaste Province, host *Liomys salvini*, field no. 0-3226, collected 3 Aug. 1964 by C. L. Hogue, R. C. Stephens and J. C. Geest; 2 paratopotypes from *Liomys salvini* (0-3228), 3 Aug. 1964; 3 paratypes from 7.3 km N Liberia, *Ototylomys phyllotis* (0-3220), 2 Aug. 1964; 2 paratypes from 5 km N Liberia, *Ototylomys phyllotis* (0-3232), 4 Aug. 1964; and 3 paratypes from 7.5 km S Liberia, 8 Aug. 1964, *Liomys salvini* (0-3291, 0-3294, 0-3295).

*Diagnosis*: Larva similar to *Pseudoschoengastia inevicta* in having 2 genualae I and genualae II and III, but differing from it in having narrower SB (13-18) and fewer (25) posterior ventral body setae (50 in *P. inevicta*).

*Description of holotype*: Body partially engorged, 143 by 218, color in life yellow; eyes 2/2, anterior larger, ocular plate present, color in life probably red.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-6-8-10-12-12-12 + 6, total 72; dorsal humeral setae 27, 25, lateral humeral seta 26, posterior dorsal seta measuring 19.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals) 19-8-8, total 31; first, second and lateral sternal setae 22, 21, 24, posterior ventral seta measuring 13 .

Scutum: elongate rectangular with sinuous posterior margin (medial portion concave), twice as wide as broad. Sensilla subcapitate.

Scutal measurements of holotype and (in parentheses) the mean, ± 2 SE and range of 11 specimens unless otherwise noted: AW, 37 (38 ± 1, 36-40); PW, 48, (51 ± 1, 47-54); SB, 15 (16 ± 1, 13-18); ASB, 19 (18 ± 1, 17-21); PSB, 9 (9 ± 0.5, 8-10); AP, 22 (22 ± 1, 20-24); AM, 26 (26 ± 1, 24-28, 6); AL 16 (16 ± 1, 15-17); PL, 27 (26 ± 1, 24-27); S, 27 (1).

Gnathosoma: cheliceral blade with tricuspid cap; cheliceral base and capitular sternum punctate. Galeala nude or with one branch. Palpal setal formula B/B/BNB.

Legs (specialized setae): leg 1 with 2 genualae; genualae II and III present.

Leg measurements of holotype and (in parentheses) the means and extremes of holotype and 10 paratypes: leg I, 180 (178, 166-189); leg II, 148 (141, 133-148); leg III, 171 (167, 159-175); leg index, 499 (482, 463-502).

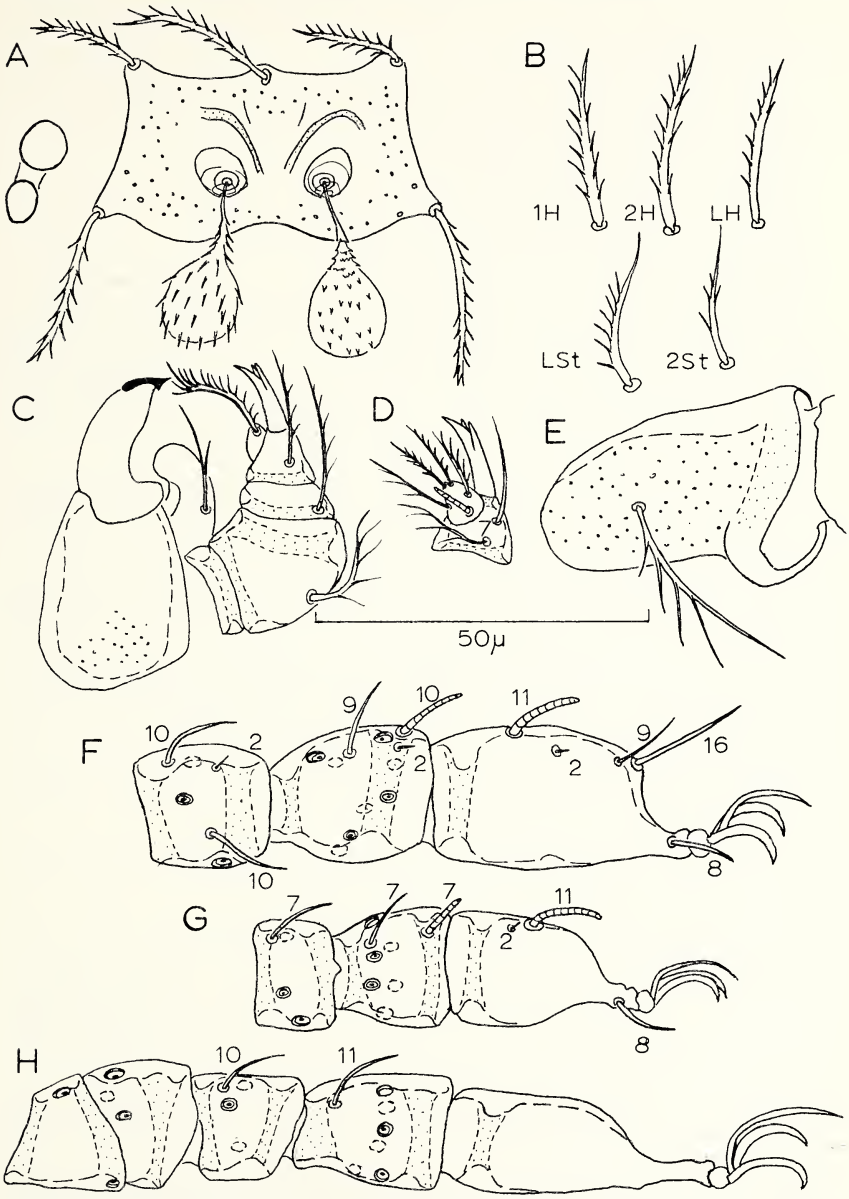



Figure 14. *Pseudoschoengastia guanacastensis* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

*Ecological notes*: Known only from the Guanacaste Biotic District off the rodents *Ototylomys* and *Liomys*.

*Specimens examined*: Total of 26 larvae: GUANACASTE: 8.3-5 km N Liberia, 3-4 Aug. 1964, *Liomys salvini* (5), *Ototylomys phyllotis* (7); 7.5 km S Liberia, 8 Aug. 1964, *Liomys salvini* (14).

## **Pseudoschoengastia costaricensis** sp. n.

Fig. 15

*Types*: Larvae, holotype and 43 paratypes: holotype and 7 paratopotypes from 2 km W Liberia, Guanacaste Province, 144 m, host *Liomys salvini*, field no. 0-415, taken 26 July 1962 by F. S. Truxal, C. A. McLaughlin, R. S. Casebeer and A. A. Schoenherr; 25 paratypes, 7.3 km S Liberia, *Liomys salvini* (0-3292), obtained 8 Aug. 1964 by C. L. Hogue, R. C. Stephens and J. C. Geest.

*Diagnosis*: Larva similar to *Pseudoschoengastia apista* in having 2 genualae I, but differing from it in lacking genualae II and III and with dorsal palpal tibial seta branched.

*Description of holotype*: Body partially engorged, 160 by 256, color in life yellow; eyes 2/2, anterior larger, ocular plate present, color in life probably red.

Dorsal setal formula 4 (humerals)-2 (lateral humerals)-8-8-4-10-12-12-10-8 + 24, total 102; dorsal humeral setae 26, 26, lateral humeral seta 26, seta of first posthumeral row 20, posterior dorsal seta measuring 19.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-4-8-8-6-2-2, total 30; first, second and lateral sternal setae 24, 22, 27, posterior ventral seta measuring 16.

Scutum: nearly rectangular with posterior margin slightly convex, sensilla clavate.

Scutal measurements of holotype and (in parentheses) the mean, ± 2 SE and range of 10 selected specimens, unless otherwise noted: AW, 41 (42 ± 1, 37-45); PW, 54 (51 ± 2, 47-56); SB, 17 (16 ± 1, 14-19); ASB, 17 (19 ± 1, 17-21); PSB, 14 (13 ± 1, 11-14); AP, 26 (25 ± 1, 22-28); AM, 27 (25 ± 1, 22-27); AL, 17 (17 ± 1, 14-20); PL, 27 (27 ± 1, 25-29); S, 31 (29 ± 1, 26-31, 6).

Gnathosoma: cheliceral blade with a tricuspid cap. Galeala with 1 to 5 branches. Palpal setal formula B/B/BNB; claw with 3 prongs, shorter prongs subequal in length.

Legs (specialized setae): leg I with 2 genualae I; genualae II and III absent.

Leg measurements of holotype, means and (in parentheses) extremes of holotype and 12 paratypes: leg I, 187, 183 (166-212); leg II, 139, 146 (128-174); leg III, 167, 171 (161-189); leg index, 493, 509 (466-575).

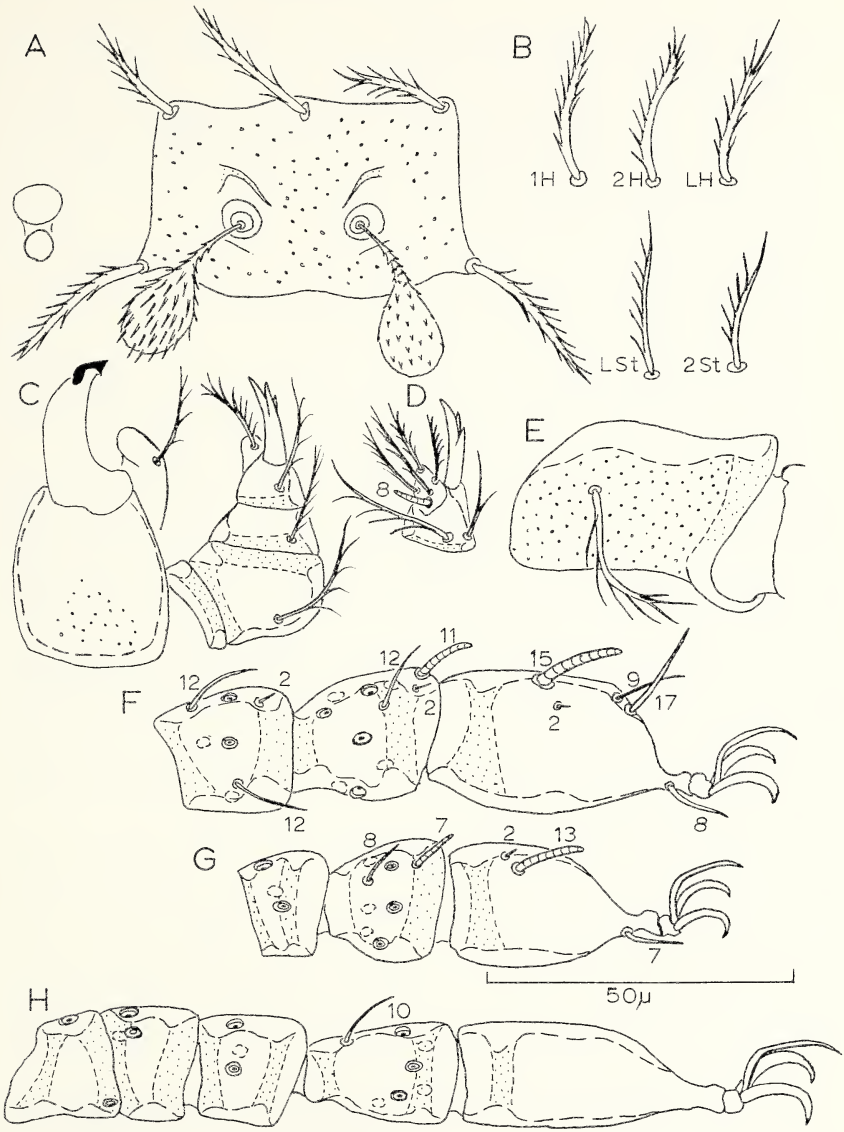



Figure 15. *Pseudoschoengastia costaricensis* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

*Ecological notes*: Except for a single larva off *Ototylomys phyllotis,* this chigger is known only from the heteromyid rodent, *Liomys,* in the Guanacaste Biotic District.

*Specimens examined*: Total of 51 larvae: GUANACASTE: 5 km N Liberia, *Ototylomys phyllotis,* 4 Aug. 1964 (1); 2 km W Liberia, *Liomys salvini,* 26 July 1962 (8); 7.3 km S Liberia, *Liomys salvini,* 8 Aug. 1964 (40); 3 km S Playa del Coco, *Liomys salvini,* 23 July 1962 (2).

## **Pseudoschoengastia verdensis** sp. n.

Fig. 16

*Types*: Larvae, holotype and single paratopotype from Monteverde, 1380 m, Puntarenas Province, host *Peromyscus nudipes,* field no. 0-3178, obtained 24 July 1964 by C. L. Hogue, R. C. Stephens and J. C. Geest.

*Diagnosis*: Larva resembling *Pseudoschoengastia apista* Brennan and Yunker (1966) in having similar scutum and same palpal setal formula B/B/NNB, but differing from it in having 1 genuala I (2 in *P. apista*) and 2 pairs of dorsal humerals (1 pair in *P. apista*); also similar to *Pseudoschoengastia mermeriza* Brennan and Yunker (1966) but latter with palpal genual seta nude.

*Description of holotype*: Body partially engorged, 180 by 265, color in life yellow; eyes 2/2, posterior larger, ocular plate present, color in life probably yellow.

Dorsal setal formula 3-3 (humerals)-4-6-6-6-6-6 $\pm$ 10, total 50; dorsal humeral setae 40, 38, lateral humeral seta 26, seta of first posthumeral row 28, posterior dorsal seta measuring 24.

Ventral setal formula 2-2 (sternals)-2 (lateral sternals)-6-8-2-4-4, total 28; first and second sternal setae lacking in specimens examined, lateral sternal setae 28, 26, posterior ventral seta measuring 14.

Scutum: shape roughly square with posterior margin sharply convex, sensilla unknown.

Scutal measurements of holotype and single paratype (in parentheses): AW, 38 (38); PW, 52 (54); SB, 20 (18); ASB, 24 (20); PSB, 16 (18); AP, 25 (25); AM, 28 (29); AL, 22 (20); PL, 29 (33); S, —.

Gnathosoma: cheliceral blade with tricuspid cap; cheliceral base and capitular sternum punctate. Galeala nude. Palpal setal formula B/B/NNB.

Legs (specialized setae as follows): leg I with 1 genuala; genualae II and III absent.

Leg measurements of holotype and single paratype: leg I, 180, 180; leg II, 151, 153; leg III, 175, 173; leg index 506, 506.

*Specimens examined*: Total of 2 larvae of type series.

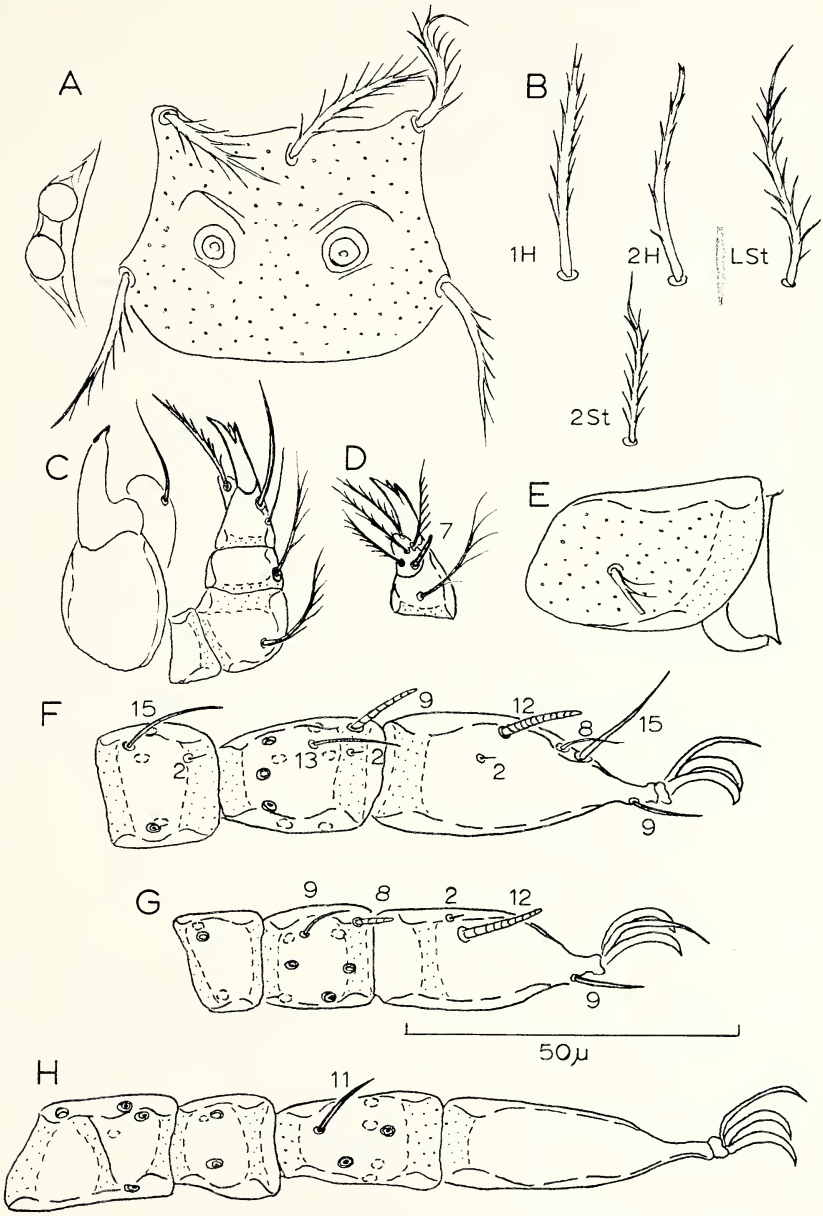



Figure 16. *Pseudoschoengastia verdensis* sp. n. A. Scutum and eyes. B. Representative body setae. C. Dorsal aspect of gnathosoma. D. Ventral aspect of palpal tibia and tarsus. E. Coxa III. F. Leg I; genu, tibia and tarsus with nude setae and bases of branched setae on genu and tibia. G. Leg II. H. Leg III; fused femur with internal bars.

## Key to the Species of *Pseudoschoengastia* from Central and South America.

1. Posterolateral setae off scutum (subgenus *Pseudoschoengastia*) ..... 2
1.[1] Posterolateral setae on scutum (subgenus *Walchioides*) ..... 16
2. Anterolateral seta > AM and PL scutal setae (Hungerfordi Group) ..... 3
2.[1] Anterolateral seta = or < AM and PL scutal setae ..... 9
3. Two genualae I ..... 4
3.[1] Three genualae I ..... 5
4.[1] Dorsal palpal tibial seta nude, lateral branched (Guatemala) ..... *P. guatemalensis* Brennan
4.[1] Dorsal palpal tibial seta branched, lateral nude (Panamá) ..... *P. dasypi* Brennan and Yunker
5. Sensilla with bulb on stem ..... 6
5.[1] Sensilla without bulb on stem (Texas, Mexico and Guatemala) ..... *P. audyi* Brennan and Jones
6. Lateral palpal tibial seta nude ..... 7
6.[1] Lateral palpal tibial seta branched ..... 8
7. Cheliceral cap serrated (Costa Rica) ..... *P. intermedia* sp. n.
7.[1] Cheliceral cap not serrated (Costa Rica) ..... *P. peromysci* sp. n.
8. Dorsal palpal tibial seta branched, 2 bars in femur III (Costa Rica and Panamá) ..... *P. bulbifera* Brennan
8.[1] Dorsal palpal tibial seta nude, 3 bars in femur III Costa Rica) ..... *P. montana* sp. n.
9. Cheliceral blade with dorsomedial tooth (Farneri Group) ..... 10
9.[1] Cheliceral blade without dorsomedial tooth ..... 13
10. Palpal genual seta branched ..... 11
10.[1] Palpal genual seta nude ..... 12
11. Dorsal and ventral palpal tibial setae branched (Costa Rica) ..... *P. rheomys* sp. n.
11.[1] Dorsal and ventral palpal tibial setae nude (Costa Rica) ..... *P. hooperi* sp. n.
12. Two genualae I, no genualae II and III (Costa Rica) .....
12.[1] Three genualae I, genuala II and III present (Costa Rica and Panamá) ..... *P. zona* Brennan
13. Cheliceral blade with small tricuspid cap (Anomala Group) ..... 14
13.[1] Cheliceral blade with large tricuspid cap (Aeci Group) ..... 15
14. One pair of dorsal humerals (Panamá) ..... *P. tricosa* (Brennan and Jones)
14.[1] Two pairs of dorsal humerals (Costa Rica and Panamá) ..... *P. abditiva* Brennan
15. One pair of dorsal humerals, eyes present (French Guiana) ..... *P. myoproctae* Fauran

15.[1] Two pairs of dorsal humerals, eyes absent (Costa Rica and Panamá).... .....*P. finitima* Brennan and Yunker
16. One genuala I.....19
16.[1] Two genualae I.....17
17. Genualae II and III present.....18
17.[1] Genualae II and III about (Costa Rica).....*P. costaricensis* sp. n.
18. One pair of dorsal humerals (Panamá).....*P. apista* Brennan and Yunker
18.[1] Two or more pairs of dorsal humerals (Costa Rica)..... .....*P. guanacastensis* sp. n.
19. Palpal genual seta nude (Panamá, Canal Zone)..... .....*P. mermeriza* Brennan and Yunker
19.[1] Palpal genual seta branched (Costa Rica).....*P. verdensis* sp. n.

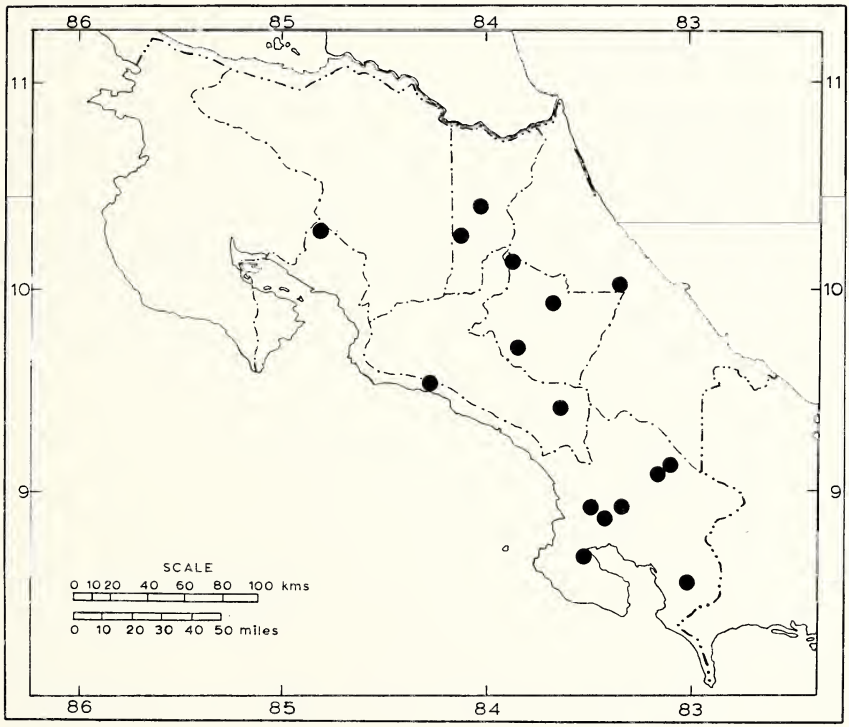



Figure 17. Locality records for *Pseudoschoengastia bulbifera*, ●.

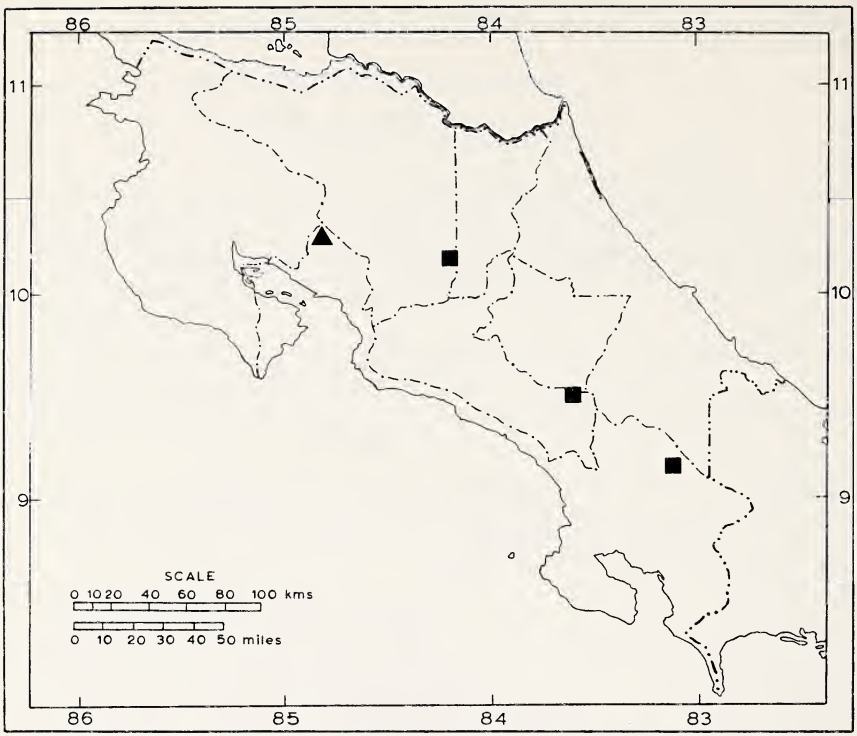



Figure 18. Locality records for *Pseudoschoengastia montana*, ■ and *P. peromysci*, ▲.

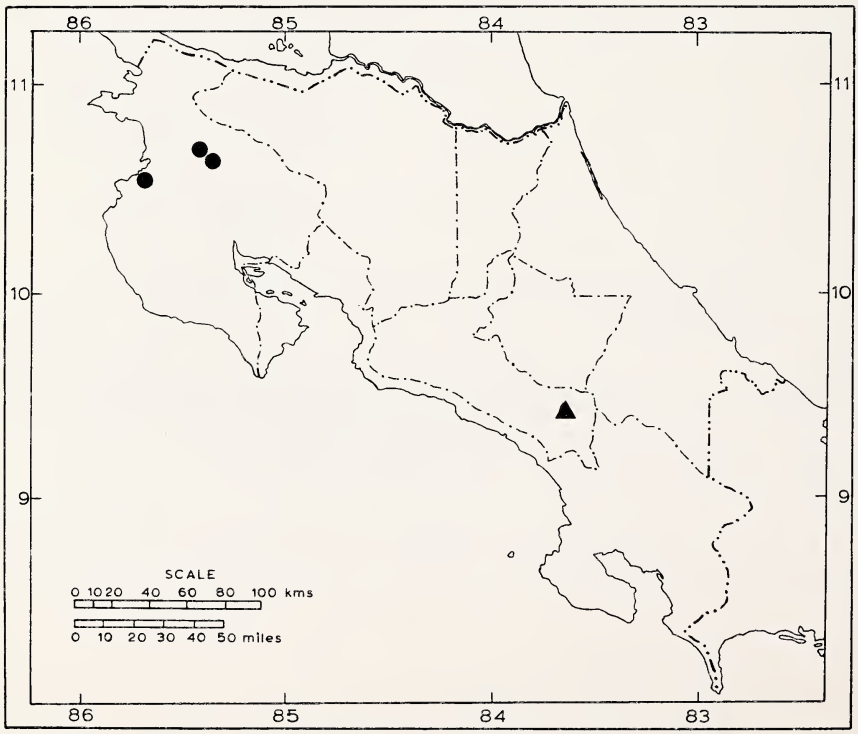



Figure 19. Locality records for *Pseudoschoengastia costaricensis*, ● and *P. intermedia*, ▲.

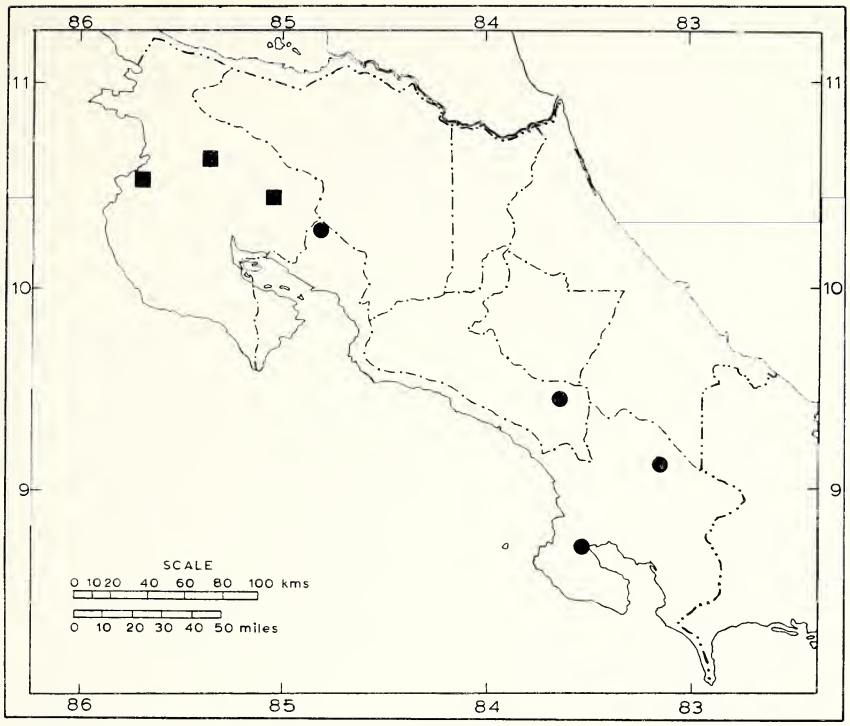



Figure 20. Locality records for *Pseudoschoengastia hoguei*, ■ and *P. zona*, ●.

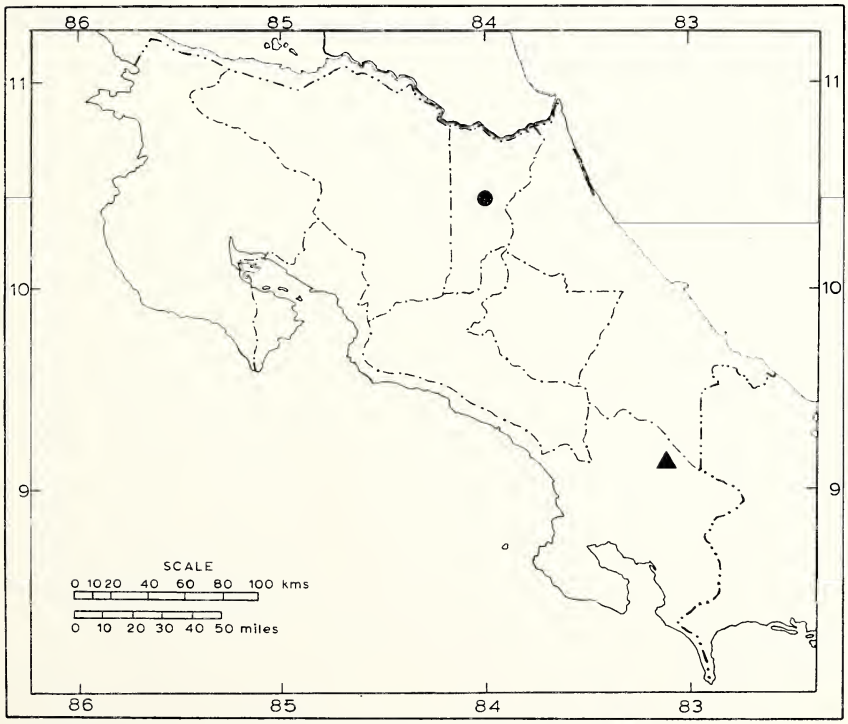



Figure 21. Locality records for *Pseudoschoengastia finitima*, ● and *P. abditiva*, ▲.

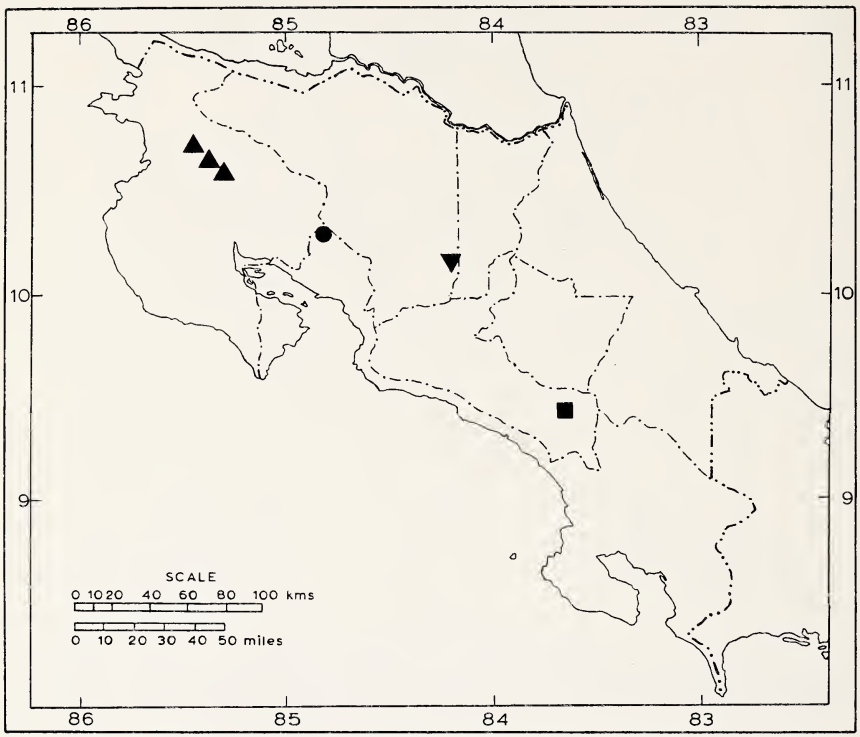



Figure 22. Locality records for *Pseudoschoengastia guanacastensis*, ▲, *P. verdensis*, ●, *P. rheomys*, ■ and *P. hooperi*, ▼.

TABLE 2

Larval characters of *Pseudoschoengastia* from Costa Rica. (For abbreviations see text.)

| *Pseudoschoengastia* | Palpal tarsal setal formula femur / genu / tibia * D-L-V | Gal-eala | Genualae I | II | III | PL's off/on scutum | D-M Chel-iceral Tooth | Bars in Femur III | AL vs PL >=< |
|---|---|---|---|---|---|---|---|---|---|
| 1. *P. bulbifera* | B / B / BBB | N | 3 | 1 | 1 | off | + | 2 | > |
| 2. *P. intermedia* | B / B / NNB | N | 3 | 1 | 1 | off | + | 2.5 | > |
| 3. *P. montana* | B / B / NBB | N | 3 | 1 | 1 | off | + | 2.5 | > |
| 4. *P. peromysci* | B / B / NNB | N | 3 | 1 | 1 | off | + | 2.5 | > |
| 5. *P. zona* | B / N / NNN | N | 3 | 1 | 1 | off | + | 2 | < |
| 6. *P. hoguei* | B / N / NNN | N | 2 | 1 | 1 | off | + | 2.5 | < |
| 7. *P. rheomys* | B / B / BNB | N | 3 | 1 | 1 | off | + | 2 | = |
| 8. *P. hooperi* | B / B / NNN | N | 3 | 1 | 1 | off | + | 2 | < |
| 9. *P. abditiva* | B / N / NNN | N | 3 | 1 | 1 | off | 0 | 2 | < |
| 10. *P. finitima* | B / N / BNB | N | 2 | 1 | 1 | off | 0 | 2 | < |
| 11. *P. guanacastensis* | B / B / BNB | N (1B) | 2 | 1 | 1 | on | 0 | 3 | < |
| 12. *P. costaricensis* | B / B / BNB | B | 2 | 0 | 0 | on | 0 | 3 | < |
| 13. *P. verdensis* | B / B / NNB | N | 1 | 0 | 0 | on | 0 | 3 | < |

*B=branched
N=nude

TABLE 3

List of Mammalian Hosts for
Species of *Pseudoschoengastia* in Costa Rica

| Species of Mammals* (number of hosts with *Pseudoschoengastia*) | Chiggers |
|---|---|
| ORDER MARSUPIALA | |
| Family Didelphidae | |
| *Philander opossum* (Linnaeus) (Four-eyed Opossum) (1) | *P. bulbifera*<br>*P. zona* |
| ORDER RODENTIA | |
| Family Heteromyidae | |
| *Heteromys desmarestianus* Gray (Desmarest's Spiny Pocket Mouse) (2) | *P. bulbifera*<br>*P. finitima* |
| *Liomys salvini* (Thomas) (Salvin's Spiny Pocket Mouse) (30) | *P. hoguei*<br>*P. guanacastensis*<br>*P. costaricensis* |
| Family Cricetidae | |
| *Oryzomys alfaroi* (Allen) (Alfaro's Rice Rat) (1) | *P. abditiva*<br>*P. bulbifera*<br>*P. montana* |
| *Oryzomys bombycinus* Goldman (Silky Rice Rat) (2) | *P. abditiva*<br>*P. montana* |
| *Oryzomys caliginosus* (Tomes) (Costa Rican Dusky Rice Rat) (24) | *P. bulbifera*<br>*P. zona* |
| *Oryzomys albigularis* (Tomes) (=*O. devius*) (Chiriqui Rice Rat) (7) | *P. bulbifera*<br>*P. intermedia*<br>*P. montana*<br>*P. zona* |
| *Oryzomys fulvescens* (Saussure) (Costa Rican Pygmy Rice Rat) (1) | *P. bulbifera* |
| *Ototylomys phyllotis* Merriam (Nicaraguan Climbing Rat) (2) | *P. guanacastensis*<br>*P. costaricensis* |
| *Peromyscus nudipes* (Allen) (Naked-footed Deer Mouse) (12) | *P. bulbifera*<br>*P. montana*<br>*P. peromyscus*<br>*P. zona*<br>*P. verdensis* |
| *Rheomys hartmanni* Enders (Panamanian Water Mouse) (6) | *P. rheomys* |
| *Rheomys underwoodi* Thomas (Costa Rican Water Mouse) (3) | *P. hooperi* |
| *Scotinomys teguina* (Alston) (Alston's Brown Mouse) (1) | *P. bulbifera* |
| *Sigmodon hispidus* Say and Ord (Hispid Cotton Rat) (5) | *P. bulbifera*<br>*P. zona* |
| *Zygodontomys microtinus* Thomas (=*Z. cherriei*) | *P. bulbifera* |
| Family Echimyidae | |
| *Proechimys semispinosus* (Tomes) (Tomes' Spiny Rat) (5) | *P. bulbifera*<br>*P. zona* |

*The specific names in this list follow Handley (1966), with previously used names in parentheses.

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# CONTRIBUTIONS IN SCIENCE

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# A NEW EARLY TERTIARY PERISSODACTYL, *HYRACOTHERIUM SEEKINSI*, FROM BAJA CALIFORNIA

*By* WILLIAM J. MORRIS

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DOROTHY M. HALMOS
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# A NEW EARLY TERTIARY PERISSODACTYL, *HYRACOTHERIUM SEEKINSI*, FROM BAJA CALIFORNIA

*By* William J. Morris[1]

Abstract: *Hyracotherium seekinsi,* a new Paleocene species from Baja California, is described as being closely related to *H. angustidens.* Rectangularity of the upper molars suggests a morphological difference between *H. angustidens, H. seekinsi,* and *Desmatoclaenus.* On the basis of rectangularity, *Desmatoclaenus* appears to be ancestral to *H. seekinsi,* but not directly ancestral to *H. angustidens.*

A sequence of red mudstone and siltstone capped by coarse conglomerate forms two small but topographically prominent buttes between Punta Prieta and Rancho Rosarito approximately 325 miles south of Ensenada in Baja California, Mexico. Five poorly preserved but significant vertebrate fossils were found at this locality during 1965 and 1966 by field parties from the Los Angeles County Museum of Natural History (LACM). In 1965 four upper molars were collected and referred to *Hyracotherium* (Morris, 1966). These molars were associated with barylambdid pantodonts and *Esthonyx* sp. The pantodonts were found approximately 20 feet above and the specimen of *Esthonyx* 30 feet below the horizon containing the molars. Since *Hyracotherium* has not been reported before as occurring with or stratigraphically below barylambdid pantodonts, it seems pertinent to stress the vertical continuity of the section. Structural complications are lacking and the strata are not overturned or faulted.

Terrestrial vertebrate fossils are rare at the Punta Prieta-Rancho Rosarito locality and, aside from the *Hyracotherium* molars, the collection includes only a partial skeleton of a barylambdid pantodont, a barylambdid pantodont scapula, various teeth of *Esthonyx* (?), and a partial skeleton of an immature creodont.

A few fresh water gastropods were collected and hackberry seeds are common.

## Acknowledgments

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Dr. Theodore Downs, Los Angeles County Museum of Natural History, reviewed the manuscript, which is more lucid as a result of his suggestions. The drawings (Fig. 1) were done by Mr. Donald Cōcke, LACM.

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My thanks to Dr. Donald Savage, Museum of Vertebrate Paleontology, University of California, Berkeley, for allowing me to study specimens from the Four Mile Creek locality.

Abbreviations used in this contribution include LACM, Los Angeles County Museum of Natural History, and AMNH, American Museum of Natural History.

## GEOLOGIC AGE OF THE PUNTA PRIETA-RANCHO ROSARITO DEPOSITS

Heim (1922) named the sequence of conglomerates, siltstones, and mudstones, outcropping near the now abandoned Rancho Tepetate, the Tepetate Formation. Later Beal (1948) extended the geographic and stratigraphic limits to include the oldest Tertiary rocks in Baja California belonging to the Paleocene and Eocene series and extending along the western side of the peninsula from San Ysidro to the latitude of La Paz. The unit is not continuous. The Punta Prieta-Rancho Rosarito outcrop is approximately 10 miles long and separated from adjacent outcrops by Late Tertiary volcanics or deep arroyos.

Invertebrates collected from a sequence lithologically similar to Punta Prieta-Rancho Rosarito, but occurring about 12 miles south of the vertebrate locality, include the gastropod, *Turritella pachecoensis,* a species characteristic of the Lower Martinez Formation considered Paleocene in the west coast invertebrate chronology.

Outcrops 60 to 70 miles north and south of the Punta Prieta-Rancho Rosarito locality have yielded Early to Middle Eocene invertebrates (Darton, 1921; Vaughn, 1929; and Beal, 1948).

Most published information, including Beal (1948), is of a preliminary nature and only gross stratigraphic units were defined.

The Baja California pantodont will be described in a later paper. Though poorly preserved, it certainly belongs in the family Barylambdidae as defined by Simons (1960). Details of the skeleton and scapula are remarkably similar to *Barylambda faberi* (Patterson, 1937) from Tiffanian Debeque Formation of Colorado. It does not resemble the Asiatic Early Eocene barylambdid, *Haplolambda planicanum.*

In a preliminary report (Morris, 1966), the Punta Prieta-Rancho Rosarito vertebrates were considered probably of Clarkforkian age. Recently Wood (1967) reviewed the evidence for a Clarkforkian fauna and found it inconclusive. He stated (p. 28), "Such evidence scarcely warrants recognition of the Clark Fork as a provincial age, faunal zone, or member of the Polecat Bench Formation." If the Clarkforkian is not valid, then the Punta Prieta-Rancho Rosarito vertebrates could be either Wasatchian or Tiffanian. The primitive nature of the *Hyracotherium* and the presence of barylambdids favor a Tiffanian Age but future discoveries may alter this conclusion.

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821

**Hyracotherium** Owen, 1840

**Hyracotherium seekinsi,** new species

*Holotype*: LACM 15349. Left $M^2$, $M^3$, and right $M^2$, $M^3$ from single maxillary. Collected by W. J. Morris field party, 1965.

*Locality and horizon*: LACM Locality No. 65155, approximately 25 kilometers south of Punta Prieta, Baja California. Locality characterized by two prominent buttes. Specimen found approximately one hundred and fifty feet below conglomerate capping most northern butte.

*Diagnosis*: $M^1$ and $M^2$ considerably smaller than those of *Hyracotherium angustidens*. Length and width of $M^3$ is within the range of *H. angustidens,* but length and width of $M^1$, $M^2$ outside the range (Fig. 3). $M^1$ and $M^2$ more rectangular than $M^3$, the greatest dimension being from the labial to lingual margins. $M^1$ and $M^2$ more rectangular than in *H. angustidens*. The principal cusps are closely appressed toward the midline, forming deep valleys between the protocone-paracone and hypocone-metacone. This feature is most conspicuous on $M^1$ and $M^2$ when compared with $M^3$.

The angle formed between the paracone and metacone margin and the posterior border is more obtuse than in specimens of *H. angustidens,* although this characteristic is notably variable among hyracotheres.

$M^1$ lacks about one-third of the labial side but a well developed protoloph and metaloph are present on the lingual side. These lophs are noticeably parallel and point towards the anterior margin of the tooth. Neither protocone nor hypocone are prominent as these two cusps form an integral part of the lophs.

Lophs are not well developed on $M^2$. The ectoloph is barely discernible between the closely appressed paracone and metacone. Both the paraloph and metaloph are sharp ridges diminishing rapidly from the paracone and metacone to the labial margin. The four major cusps are sharply pointed and stand well above the lophs. The protocone and hypocone are conical and separated by a deep depression. The labial side of both metacone and protocone slopes less steeply than the lingual side. The two cusps, geometrically, form a piercing, almost shearing blade. The parastyle of $M^2$ is compressed and crowded against the paracone.

The sharp definition of the principal cusps and the lack of loph development on $M^2$ and $M^3$ is very different from the semi-parallel strong loph development on $P^4$. $M^2$ and $M^3$ resemble *H. angustidens* and condylarths much more than does $M^1$.

It is difficult to assess the taxonomic significance of the cusps on $M^3$, as in *Hyracotherium* these are variable in geometry and position. The number and arrangement of cusps on the posterior lingual margin of $M^3$ of *H. seekinsi,*

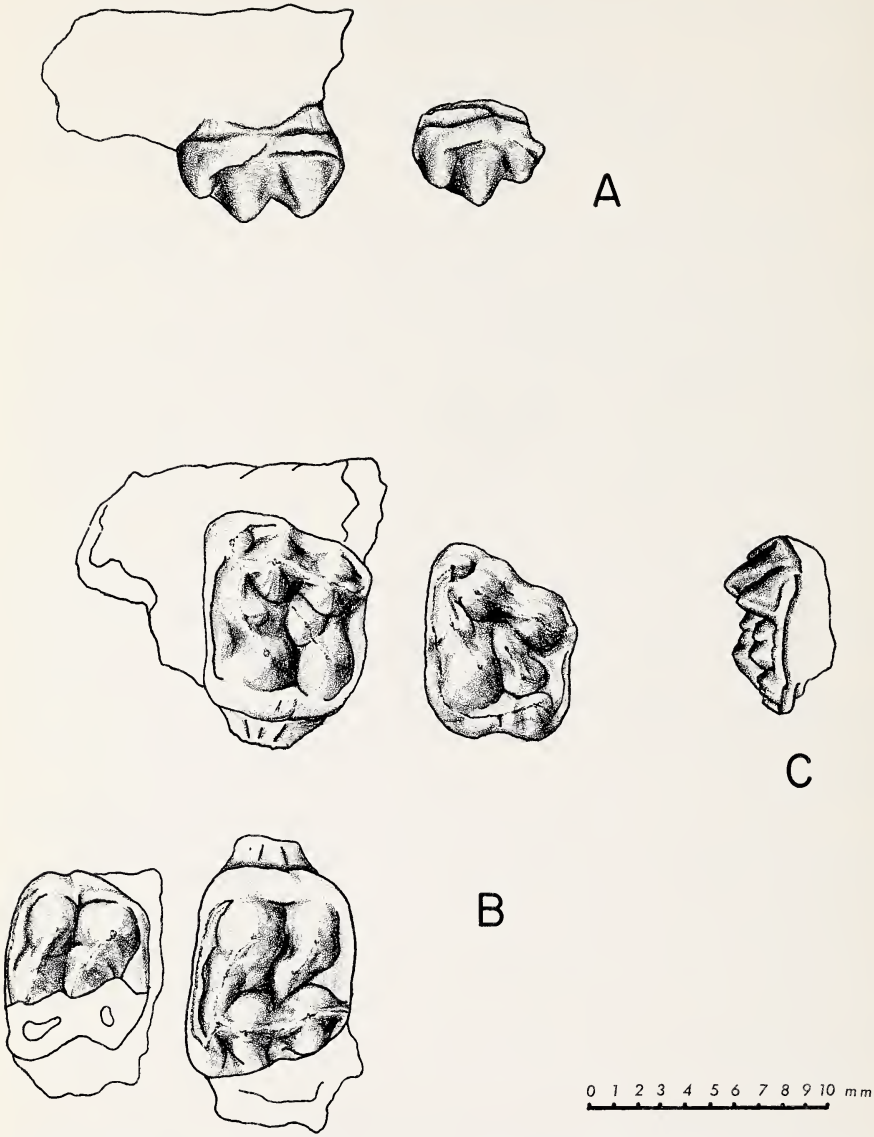


Figure 1. *Hyracotherium seekinsi*, n. sp.; A, upper left $M^2$-$M^3$ labial side; B, occlusional view upper left $M^2$-$M^3$ and upper right $M^1$-$M^2$; C, upper left $M^3$ posterior view.

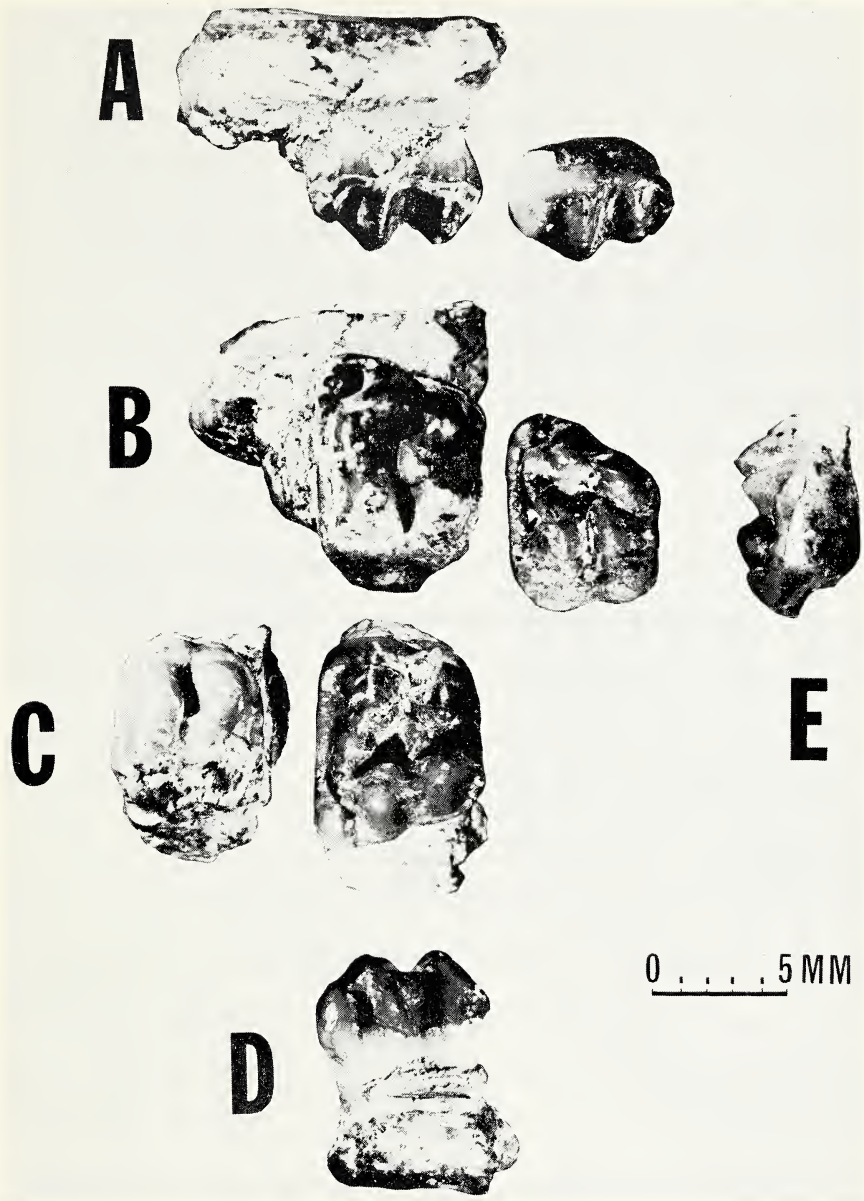


Figure 2. *Hyracotherium seekinsi*, n. sp.; A, upper left $M^2$-$M^3$ labial aspect; B, occlusional view upper left $M^2$-$M^3$; C, occlusional view upper right $M^1$-$M^2$; D, upper right $M^2$ labial aspect; E, upper left $M^3$ posterior view.

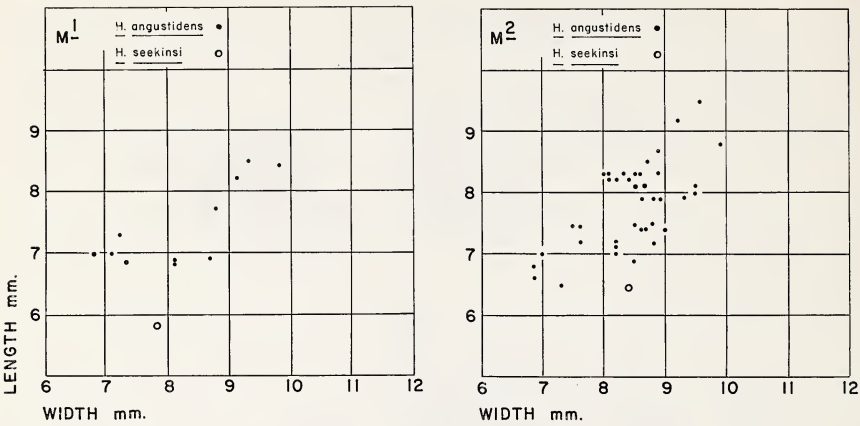


Figure 3. Scatter diagram comparing individual upper molar length-width ratios of *Hyracotherium seekinsi*, n. sp., with *H. angustidens* (Four Mile Creek).

however, do seem significant. Posterior from the protocone are two cusps located on the platform of the tooth. A third cusp, arising from the lingual cingulum, is also well developed. It is difficult to decide which of these represents the hypocone, but regardless of the cusp selected the hypocone is appreciably smaller than in observed specimens of *H. angustidens*.

This new species is named in honor of its discoverer, Mr. William Seekins.

*Discussion*: It is becoming increasingly apparent that Early Tertiary perissodactyls and their progenitors among the Paleocene condylarths are morphological intergrades, at least as regards dentition. It is impossible to ascertain the degree and kind of morphological overlap until many more geographically and temporally isolated samples have been examined. As a result it becomes extremely difficult to formulate precise parameters of diagnostic taxonomic value at the species level. This is particularly valid for *Hyracotherium seekinsi*, which may well be representative of a morphological grade between certain Paleocene condylarths and *H. angustidens*.

The condylarths, *Tetraclaenodon* and *Desmatoclaenus*, have each been proposed as progenitors of *Hyracotherium*. Apparently neither geometry nor number of cusps precludes either from this ancestral possibility (Kitts, 1956; Radinsky, 1966). Both condylarth genera have the necessary primary cusps to provide a morphological ancestor for *Hyracotherium*. The geometry of the teeth, aside from rectangularity (to be discussed later), appears quite different in *Hyracotherium*, *Tetraclaenodon*, and *Desmatoclaenus*. The upper molars of *Tetraclaenodon* are broadly ovate, while those of *Desmatoclaenus* are triangular. The difference is partly due to the development of at least an incipient hypocone on $M^1$ and $M^2$ of some samples of *Tetraclaenodon*, as well as the strong posterior cingulum of $M^3$. In addition, the protocone has

developed directly labial to the paracone so that lines drawn through paracone-protocone crests and metacone-hypocone crests are parallel. This is not the case in the more triangular molars of *Desmatoclaenus,* particularly in *D. hermaeus,* as the protocone is located at the V formed by the three principal cusps. The geometry of *Tetraclaenodon* is in this respect more like *Hyracotherium* than is that of *Desmatoclaenus. Hyracotherium seekinsi* shows the characteristic development of parallelism of the principal cusps on $M^1$ and $M^2$, but the teeth are much more rectangular than in *Tetraclaenodon.*

Aside from the geometry of the principal cusps, *H. seekinsi* has many morphological features suggestive of desmatoclaenid affinities. *Desmatoclaenus hermaeus* has a respectable parastyle on $M^2$ that is closely appressed against the paracone and connected to it by an anterior spur of the ectoloph. This is almost a duplicate of the morphological condition in $M^2$ of *Hyracotherium seekinsi.* In addition, $M^2$ of both *Desmatoclaenus hermaeus* and *Hyracotherium seekinsi* have protoconules and metaconules less developed than in primary cusps, paracone and metacone appressed towards the midline, and slight development of the ectoloph between paracone and metacone. Another feature common to the two genera is the similarity of the protoloph, which trends in an anterior direction towards the parastyle, gradually diminishing in height and interrupted midway by a modestly developed protoconule. $M^3$ of *Hyracotherium seekinsi* has three weakly developed cusps or cuspules on the hypocone portion. Were these not present, the tooth would show a striking resemblance to the $M^3$ of *Desmatoclaenus hermaeus.* It is feasible that the hypocone of the *Hyracotherium* lineage arose from a strong posterior labial cingulum similar to the one present on $M^3$ of *Desmatoclaenus hermaeus.*

## COMPARATIVE RECTANGULARITY OF TEETH

*Hyracotherium seekinsi* is morphologically similar to *H. angustidens* and temporally near this species. The problem of whether *H. seekinsi* is ancestral to the later *H. angustidens* or is representative of a variant population of early perissodactyls cannot be solved from a few teeth. Kitts (1956) demonstrates that *H. angustidens* consists of several intergrading populations closely related but not of proven contemporaneity. Aside from central measurements of size frequency, definitive molar characteristics have not been recognized for these populations. Molar comparison of *H. seekinsi* with *H. angustidens* shows a marked difference in rectangularity. That may reasonably be of phylogenetic importance as well as of diagnostic value.

Rather than using scatter diagrams to portray rectangularity, a more direct method of comparison has been used (Figs. 4, 5). Linear measurements were made for each specimen and the mean length and mean width computed when warranted by the size of the sample. A line from the origin to a point determined by the coordinates of mean length and width was drawn

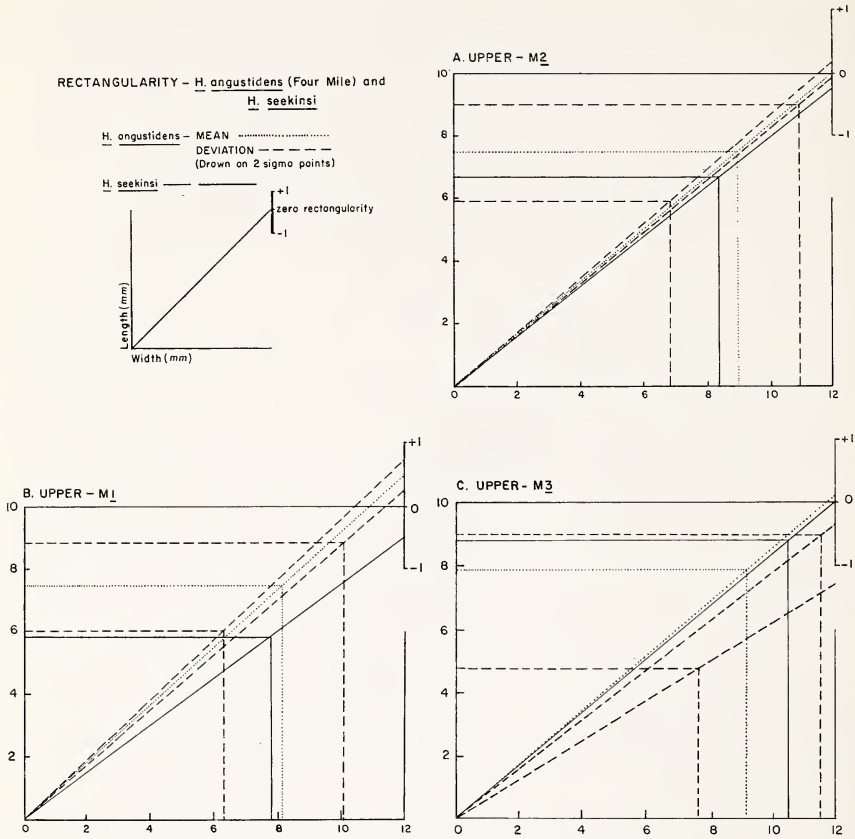


Figure 4. Diagram illustrating graphic method of compiling comparative rectangularity measures as presented in Figure 5. Upper molars of *Hyracotherium seekinsi* (solid line) are compared with *H. angustidens* (dashed and dotted lines) from the Four Mile Creek localities; for *H. angustidens*, $M^1$ N = 7, $M^2$ N = 34, $M^3$ N = 32. Upper left diagram shows parameters for diagram A-C. Figure 5 contains only the rectangularity scale. The measure of rectangularity adopted is comparative only when the same scale is used for all included teeth.

Note that in *size,* as indicated by the dotted, dashed and solid outlined rectangles, the *H. seekinsi* molars fall within or close to two standard deviations of *H. angustidens*, whereas the measure of rectangularity more clearly expresses a difference between these teeth.

and extended a convenient distance. An arbitrary scale from plus 1 to minus 1 was adopted as a measure of rectangularity. Fig. 4 illustrates the graphic method used in establishing the measure of rectangularity. Comparisons of the rectangularity of taxa under consideration are presented in Fig. 5. When

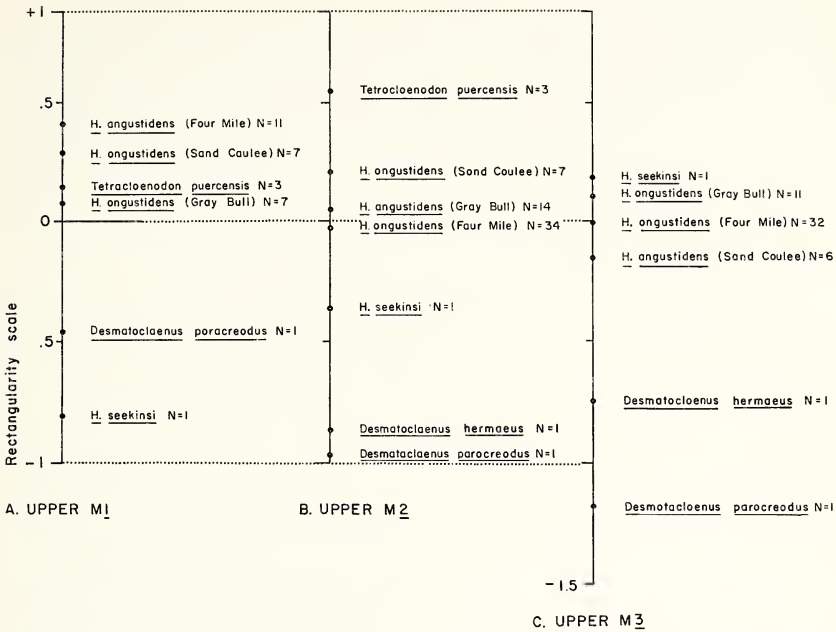


Figure 5. Relative rectangularity of selected species of Early Tertiary perissodactyls and condylarths. *Desmatoclaenus paracreodus* is included to show the closer morphological similarities of *D. hermaeus* to *Hyracotherium seekinsi.*

rectangularity is presented in this manner, it is independent of size as long as the same scale is used in the comparison.

$M^1$ and $M^2$ of *Hyracotherium seekinsi* are more rectangular than those of *H. angustidens,* although in both species the teeth are short and wide. This difference in rectangularity appears to be a consistent one, as shown in *H. angustidens* samples from Four Mile Creek (University of California, Berkeley, V5365E, V5350, V5396, V5424, V5421, V5422, V5357), Sand Coulee and Graybull populations (measurements taken from Kitts, 1956). There is no significant difference in rectangularity between $M^3$ of *Hyracotherium seekinsi* and *H. angustidens.*

Three specimens of *Tetraclaenodon* from the upper Nacimiento Formation (AMNH 15927), one of *Desmatoclaenus hermaeus,* and one of *D. paracreodus* (Gazin, 1941), were plotted. While certainly not conclusive, the plots provide interesting comparisons with *Hyracotherium seekinsi* (Fig. 3).

Rectangularity exhibited in $M^1$ and $M^2$ of *Tetraclaenodon* does not differ from that of *Hyracotherium angustidens.* It does differ considerably from the rectangularity of $M^1$ and $M^2$ of *H. seekinsi.*

*Desmatoclaenus hermaeus* and *D. paracreodus* have the most rectangu-

lar $M^1$ and $M^2$ when compared to *Hyracotherium angustidens, H. seekinsi* and *Tetraclaenodon. Hyracotherium seekinsi* may well belong in the direct lineage leading to *H. angustidens,* and, in turn, could more reasonably be derived from *Desmatoclaenus* than from *Tetraclaenodon.* This supposition is suggested by the rectangularity of the anterior molars and strengthened by the biostratigraphic positions of the genera. It is also possible that *Hyracotherium seekinsi* is a representative from an isolated population evolving from desmatoclaenid condylarths, while *H. angustidens* evolved from condylarths closer to tetraclaendontids.

$M^3$ of *Tetraclaenodon, Hyracotherium angustidens,* and *H. seekinsi* has about the same degree of rectangularity. *Desmatoclaenus,* on the other hand, has a very rectangular $M^3$. This may be indicative of a primitive characteristic that was lost when the perissodactyl level of organization was attained.

## CONCLUSIONS

*Hyracotherium seekinsi* differs from *H. angustidens,* its closest morphological relative, in a number of details of cusp geometry in the upper molars, as well as in rectangularity of $M^1$ and $M^2$. *Hyracotherium seekinsi,* or a species much like it, could very well be ancestral to *H. angustidens.* On the other hand, *Hyracotherium seekinsi* may represent a population not on the lineage from a condylarth progenitor to *H. angustidens.* These are important considerations, as *Hyracotherium seekinsi* is certainly, morphologically, more like *Desmatoclaenus* than like *Tetraclaenodon.* If *Hyracotherium seekinsi* is ancestral to *H. angustidens,* then *Desmatoclaenus* is a more satisfactory morphological ancestor for these Early Tertiary perissodactyls than is *Tetraclaenodon.*

Radinsky (1966, p. 408) states that if ". . . protoperissodactyls and *Tetraclaenodon* were independently derived from a still more primitive common ancestor, [this hypothesis] requires an additional complicating factor—an independent acquisition of molar hypocones by perissodactyls and phenacodontids." Gazin (1941) however, does regard *Desmatoclaenus hermaeus* as having a weak hypocone, but not well developed when compared to that of *Tetraclaenodon.*

*Hyracotherium angustidens* is morphologically more like *Tetraclaenodon,* and *Hyracotherium seekinsi* more like *Desmatoclaenus hermaeus.* Either the hypothesis of a desmatoclaenid-*H. seekinsi-H. angustidens* lineage is tenable or independent derivation of *H. seekinsi* and *H. angustidens* appears necessary.

## RESUMEN

Un nuevo perisodáctilo encontrado en depósitos que pertenecen a inicios del Terciario se describe como una nueva especie, *Hyracotherium seekinsi.* Este está relacionado de cerca con *H. angustidens.* La rectangularidad de los molares superiores sugiere diferencias morfológicas entre *H. angustidens, H. seekinsi* y

*Desmatoclaenus*. De acuerdo con este criterio de rectangularidad, *Desmatoclaenus* parece ser un ancestro de *H. seekinsi*, sin embargo, no parece ser un ancestro directo de *H. angustidens*.

Esta descripción de *H. seekinsi* se basa en único molar colectado aproximadamente 25 Km. al Sur de Punta Prieta, Baja California. Se incluyen ilustraciones de los dientes.

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LOS ANGELES COUNTY MUSEUM

# CONTRIBUTIONS IN SCIENCE

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# A NEW CENTRAL AMERICAN SAND FLY BREEDING IN CRAB HOLES (DIPTERA, CERATOPOGONIDAE)

*By* CHARLES L. HOGUE AND WILLIS W. WIRTH

SMITHSONIAN

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MANUSCRIPT FORM.—(1) the 1964 AIBS Style Manual for Biological Journals is highly recommended as a guide. (2) Typewrite material, using double spacing throughout and leaving ample margins, on only one side of 8½ x 11 inch standard weight paper. (3) Place tables on separate pages. (4) Footnotes should be avoided if possible. (5) Legends for figures and unavoidable footnotes should be typed on separate sheets. Several of one kind may be placed on a sheet. (6) A factual summary is recommended for longer papers. (7) A brief abstract must be included for *all* papers. This will be published at the head of each paper.

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DOROTHY M. HALMOS
*Editor*

# ERRATA

The Editor and Editorial Committee

# ERRATA

The Editor and Editorial Committee of the Los Angeles County Museum of Natural History Contributions in Science regret that three references to scale of illustrations were incorrectly designated in OCCURRENCE OF A GIANT BISON, *Bison latifrons*, AND A SLENDER-LIMBED CAMEL, *Tanupolama*, AT RANCHO LA BREA, Los Angeles County Museum *Contributions* in Science, number 147.

The corrections should read as follows:

| Page | Figure | Published scale | Corrected scale |
|---|---|---|---|
| 2 | 1 | 1-1/2 | 1 |
| 5 | 3 | 1/2 | 1/4 |
| 6 | 5 | 1/2 | 1/4 |

We also take this opportunity to stress that you make these changes in your copy of Contributions 147 rather than insert this mimeographed sheet.

We regret these inconveniences.

Dorothy M. Halmos,
Editor

Robert J. Lavenberg,
Managing Editor

# A NEW CENTRAL AMERICAN SAND FLY BREEDING IN CRAB HOLES (DIPTERA, CERATOPOGONIDAE)

*By* Charles L. Hogue[1] and Willis W. Wirth[2]

Abstract: The larva, pupa, and adult of a new species of sand fly, *Culicoides cancer*, are described and figured from material collected in Costa Rica. The species is a member of the Furens Group but is unique in its lack of anthropophily and in its breeding site, the burrows of the land crab, *Cardisoma crassum*.

Sand flies of the genus *Culicoides* almost universally utilize, as their larval habitat, the shore lines of tidal swamps and estuaries where they often become extremely numerous. If the females of the species show a preference for human blood, they may become almost intolerable pests when man invades this environment. One group of salt marsh sand flies which has become notorious in the American tropics is the Furens Group, which contains four species, *C. furens* (Poey), *C. barbosai* Wirth and Blanton, *C. gorgasi* Wirth and Blanton, and *C. alahialinus* Barbosa, all causing annoyance to man.

The senior author recently discovered a fifth member of this group living in crab holes on the Pacific coast of Costa Rica. During the six-week period of these investigations, this crab hole species was never observed to bite man, although *C. gorgasi* and *C. barbosai* (during other periods in the study area) were frequently taken while biting. *Culicoides furens* has been collected while biting man at Golfito, also on the Pacific coast of Costa Rica.

At Boca de Barranca, Golfo de Nicoya, and at Playas del Coco, Peninsula de Nicoya, the new species, which we are naming *C. cancer* because of its association with land crabs, was collected and reared from 36 separate collections from burrows of the mouthless crab, *Cardisoma crassum* Smith, and from one burrow of the wide red land crab, *Ucides occidentalis* (Ortmann). It was not found on the Atlantic coast, but two collections from burrows of *Cardisoma guanhumi* Linnaeus at Cahuita (22 miles south of Limón) yielded a species of another group, *Culicoides reticulatus* Lutz, which has been reared from crab holes in Brazil (Forattini, Rabello, and Pattoli, 1958). A third species, *C. arubae* Fox and Hoffman, has been reported from crab holes in the Dutch West Indies (Fox, 1942: 420; Fox and Hoffman, 1944: 109), but according to Jones and Wirth's (1958) observations in Texas, it is more likely to be found in open salt water pools.

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**Culicoides cancer** new species
(Figs. 1-13)

*Diagnosis*: This species is most similar to *Culicoides gorgasi* Wirth and Blanton, but may be separated as follows:

| | *gorgasi* | *cancer* |
|---|---|---|
| Antennal sensorial pattern | 3, 8-10 | 3, 6-10 |
| Halter color | dark | pale |
| Leg bands | faint | dark |
| Apices wing veins $M_2$ and $M_{3+4}$ | dark | pale |
| Female eyes | contiguous | narrowly separated |
| Female spermathecae necks | not tapered | tapered |
| Male parameres | no ventral lobe | large ventral lobe |
| Male aedeagus | simple tip | 3-pointed tip |
| Male apicolateral processes | short | long |

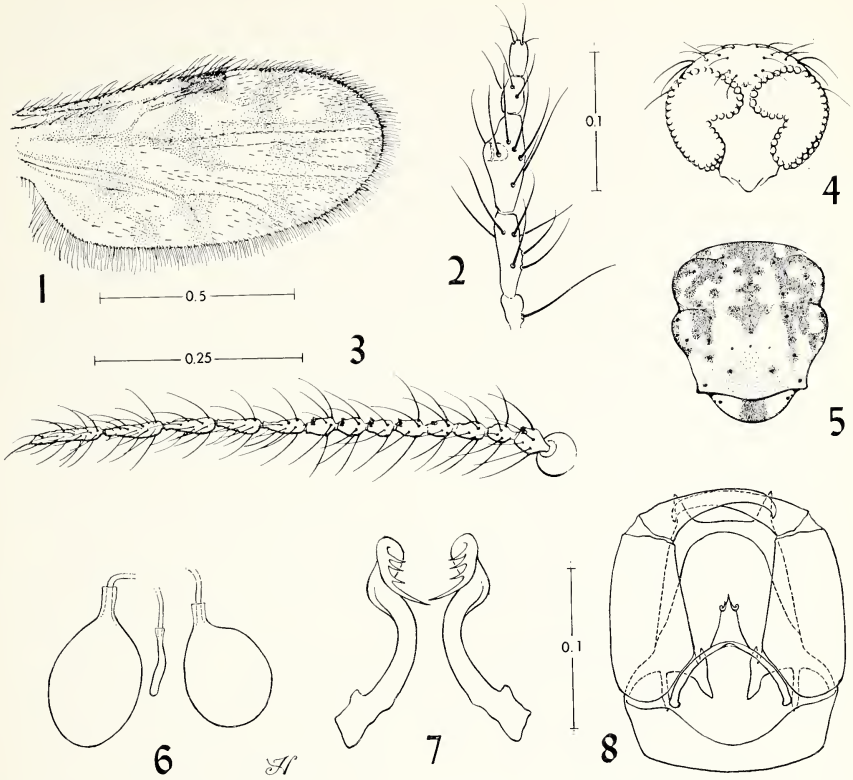
*Description* (terminology and abbreviations follow Jamnback, 1965: 15-20):

FEMALE. Length of wing 0.91 mm, breadth 0.45 mm.

Head: Eyes (Fig. 4) bare, separated by a distance equal to the diameter of an eye facet. Antenna (Fig. 3) with lengths of flagellar segments in proportion of 16-12-13-13-14-13-13-13-19-20-23-26-35, AR 1.14; distal sensory tufts present on segments three (two per segment), six (one), seven to ten (three per segment). Palpal segments (Fig. 2) with lengths in proportion of 5-10-12-5-5; third segment moderately swollen, with a small, round, moderately deep, sensory pit; PR 2.4. Proboscis moderately long, P/H ratio 1.2; mandible with 16 teeth.

Thorax: Yellowish brown; scutum with prominent pattern (Fig. 5) of dark brown punctures at bases of the coarse, sparse, setose vestiture; scutellum pale on sides, dark brown in middle; postscutellum and pleuron brown. Legs brown, knee spots blackish; trochanters and bases of femora pale; femora with subapical, and tibiae with subbasal, narrow pale rings, hind tibia pale on distal fourth; hind tibial comb with four spines, the one nearest the spur the longest.

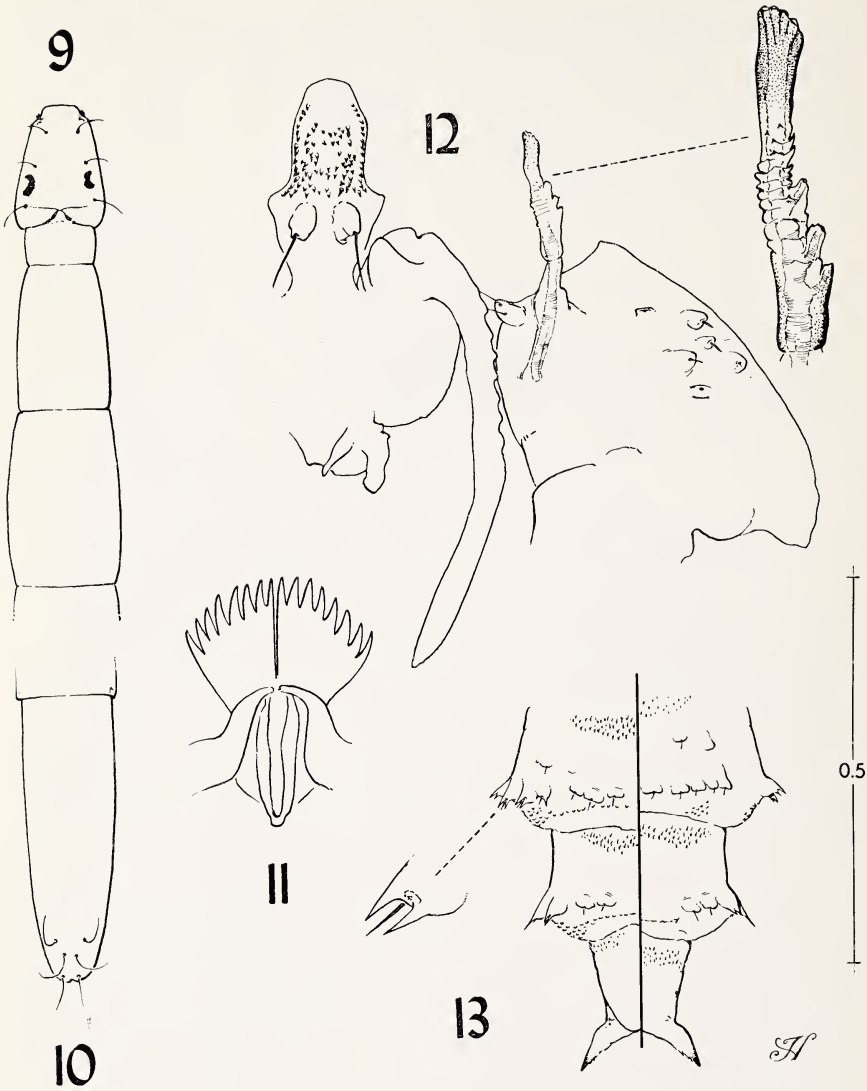
Wing (Fig. 1): Pattern as figured, pale spots distinct, creamy colored; second radial cell dark to tip; base of wing broadly pale except at basal arculus; large pale spot over r-m crossvein extending broadly from costa to media; post-stigmatic pale spot small, confined to anterior wing margin just past second radial cell; a second, separate, elongate pale area lying behind it on anterior side of vein $M_1$ and extending proximad for length of second radial




Figures 1-8. *Culicoides cancer* n. sp. 1-6, Female: (1) wing; (2) palpus; (3) antenna; (4) eye separation; (5) thoracic pattern; (6) spermathecae. 7-8, Male: (7) parameres; (8) genitalia, parameres removed.

cell; distal pale spot in cell $R_5$ large, quadrate to trapezoidal in form, extending broadly from anterior wing margin to vein $M_1$; cell with two elongate pale spots, the second continued as a narrow line to wing margin; cell $M_2$ with pale streak from base to level of middle of cell $M_4$, a separate, large, rounded pale spot apically at wing margin; cell $M_4$ with large rounded pale area broadly meeting wing margin; anal cell with two distal pale spots and pale streaks basally and at margin on anal angle; vein $M_1$ pale bordered more than halfway to base, apices of veins $M_2$ and $M_{3+4}$ with small pale spots at wing margin. Macrotrichia moderately dense and long on distal portion of wing, continued very sparsely to bases of cell $M_2$ and anal cell; CR 0.6; radial cells with distinct lumens. Halter pale.

Abdomen: Brownish. Spermathecae (Fig. 6) two, plus rudimentary third




Figures 9-13. *Culicoides cancer* n. sp. 9-11, Larva: (9) head and thorax; (10) terminal segments and setae; (11) frontoclypeus. 12-13, Pupa: (12) thorax and head sclerites; (13) terminal abdominal segments.

and sclerotized ring; slightly unequal in size, measuring 0.065 mm by 0.038 mm and 0.053 mm by 0.035 mm; ovoid in shape with very long, tapering, slender necks.

MALE. Similar to the female with the usual sexual differences; antennal plumes well developed. Genitalia (Figs. 7-8): Ninth sternum with moderately broad and deep caudomedian excavation, the ventral membrane bare; ninth tergum moderately long and slightly tapering, with moderately long and slender, pointed, slightly divergent, apicolateral processes, the caudal margin between them slightly convex. Basistyle moderately slender, slightly tapering, ventral root foot-shaped, with well-developed caudal heel and sharp anteromedian toe; dorsal root slender; dististyle slender and gradually curved, with abruptly bent, sharp tip. Aedeagus with broad, rounded, anterior basal arch extending to 0.6 of total length, the basal arms slender; distal portion broad on shoulders, tapering distally, with three subequal sharp points apically, the lateral pair abruptly bent ventrad. Parameres (Fig. 7) each with small basal knob, stem slender and sinuate, subapically with a small ventral lobe; distal constricted portion bent ventrad and mesad and tapering to sharp point with fringe of four to five sharp lateral spines.

MATURE LARVA (Figs. 9-11). Head pale yellow, elongate, length of frontoclypeus 130 (n = 3) microns; comb with 5-8 (average 6.8, n = 9) teeth on each side. Thorax without pronounced pigmented areas. Setae on last segment as figured.

PUPA (Figs. 12-13). Respiratory horn light brown, similar in color to rest of pelt except slightly darkened apically and basally, typically with four apical and three lateral spiracular openings on pronounced protuberances, with weak transverse convolutions at midlength, without spines; horn slender, widest near base, Length/Width ratio 6.3-7.2. Operculum with short, broad-based spines abundant over most of surface; *am* setae about one-half as long as maximum width of operculum. The *d* tubercles arranged as figured, setae 1 and 2 short and heavy, not overlapping; seta 4 short. Abdomen with *lmp* tubercles bifid with sharp points and a subapical seta. Last segment with sparse weak spines cephalad, none on disc; caudal apicolateral processes with a few spines caudad, apex only darkened, directed caudad at an angle of approximately 40 degrees to the longitudinal axis of the body.

*Distribution*: Pacific coast of Costa Rica.

*Material*: HOLOTYPE. Female, allotype male, Boca de Barranca, Golfo de Nicoya, Puntarenas Prov., Costa Rica, 27 June 1967, C. L. Hogue and D. B. Bright, reared from burrow of *Cardisoma crassum*, LCBA 111 (deposited in Los Angeles County Museum of Natural History).

PARATYPE. 21 males, 18 females, same data as holotype, except dates 20 June to 11 July 1967 (LCBA 2, 11, 112, 126, 147, 135, 142, 177, 111, 160, 142). Also one male, one female, same data but from burrows of *Ucides*

*occidentalis*, 10 July 1967 (field no. CR 240). Also five males, one female, Playas del Coco, Peninsula de Nicoya, Guanacaste Prov., 18 July 1967, C. L. Hogue and D. B. Bright, from burrows of *C. crassum* (LCBA 230).

ADDITIONAL MATERIAL. Numerous specimens, primarily of larvae and pupae, Boca de Barranca, Golfo de Nicoya, Puntarenas Prov., Costa Rica (LCBA collections as follows: 2, 3, 11, 104-106, 111-112, 123-126, 135, 137-139, 141-144, 147-150, 159-161, 163-165, 167-168, 170-171, 177) and Playas del Coco, Peninsula de Nicoya, Guanacaste Prov., Costa Rica (LCBA 205 and 230). All collected by C. L. Hogue and D. B. Bright.

*Biology*: All of the present material was collected during mid-rainy season in burrows of moderate to large diameter (1.5 to 5 inches) occupied by half-grown to mature crabs. The larvae were extremely numerous at times, breeding in the water which collects from ground water seepage and rainfall. The burrow water varied considerably in solute concentrations, depending on the proximity of a particular burrow to, and the nature of, a nearby water source (fresh-water stream, tidal inlet, tidal mangrove thicket or the open sea). Immatures were collected primarily from burrow water with low salt concentrations (ranging from 15-580 ppm NaC1) though they were frequently found, sometimes thriving in dense numbers, in water with moderate (1900-8600 ppm NaC1) or even high (13,000-26,000 ppm NaC1) salt concentrations. A few burrows emitted strong sulfide odors and contained black water, indicating that considerable organic decomposition was taking place therein; though in most cases the water was less putrid, it was always turbid (dark brown to grey in color) and rich in organic matter (principally plant fragments brought into the burrow by the crab host).

The foregoing indicates that the larvae and pupae of this species have a wide range of tolerance in regard to variation in the chemistry of its medium. This tolerance is shared by most of its associates and appears to be a general characteristic of estuarine and crabhole invertebrates, doubtless an adaptation permitting them to survive the extreme fluctuations, mainly in salt concentration, common to their environment.

Associated with *Culicoides cancer* at Boca de Barranca and Playas del Coco were crabhole mosquitoes (*Deinocerites pseudes* Dyar and Knab, and *Deinocerites* sp. A. Belkin and Hogue), *Culex inflictus* Theobald, unidentified water mites, and the larva of an unidentified marsh beetle (Helodidae).

Adult *Culicoides cancer* rest on the walls of the burrow throat and mouth. They are agitated readily by debris falling into the burrow and by any object (such as an aspirator) being thrust into the burrow. Under these circumstances they crawl rapidly over the soil inside the burrow and fly swiftly out of the burrow mouth, landing on the soil surface or vegetation very close by. They do not hover about the opening attempting to return, a habit often displayed by *Deinocerites*. On no occasion did specimens attempt to bite the senior author while he was collecting.

*Acknowledgments*: The material upon which this paper is based was collected as a part of a general study of the biology of land crabs and their burrow associates (LCBA) being conducted by the senior author and Donald B. Bright, California State College, Fullerton, with the support of a grant from the American Philosophical Society. The collections of *Culicoides barbosai* reported upon herein were made incidentally to a mammalian ectoparasite survey of Costa Rica (Los Angeles County Museum of Natural History) under grant numbers DA-MD-49-193-62-G54 and -63-G94, U. S. Army Medical Research and Development Command.

## SUMARIO

Las larvas, pupas y adultos de una nueva especie de jején, *Culicoides cancer*, han sido descritas y dibujadas basadas en ejemplares colectados en Costa Rica. Este especie es un miembro del Grupo Furens pero se diferencia en su falta de antropofalia y en el medio que usa para desarrollarse, el cual es en los agujeros del cangrejo terrestre, *Cardisoma crassum*.

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# A NEW PICULET FROM SOUTHEASTERN PERU

*By* KENNETH E. STAGER

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DOROTHY M. HALMOS
*Editor*

# A NEW PICULET FROM SOUTHEASTERN PERU

*By* Kenneth E. Stager[1]

Abstract: A new species of *Picumnus* from southeastern Peru is described and named *Picumnus subtilis*. The relationships of *Picumnus subtilis* and *Picumnus castelnau* are discussed.

During a revisional study of the neotropical pygmy woodpeckers of the genus *Picumnus*, an undescribed species has been found and, in anticipation of the complete revision of this genus, is named as follows:

## **Picumnus subtilis**, new species

*Holotype*: Adult male, Figs. 1-2, collected at Hacienda Villacarmen, Department of Cuzco, S. E. Peru, at an elevation of 1000 meters (3280 ft), July 9, 1958, by Emmet R. Blake. FMNH 251769.

*Diagnosis*: Closely resembles and previously confused with *Picumnus castelnau* of northern and central Peru. Is readily distinguished from this species, however, by possession of distinct white spotting on the crown and nape and by the presence of barring on the chest. These characters are in direct contrast to the immaculate crown and chest of *Picumnus castelnau*.

*Description of Type*: (Capitalized color terms are those of Ridgway, 1912.) Crown and nape deep black with each feather tipped with white or Orange Chrome. Feathers tipped with Orange Chrome extend from nasal area posteriorly for at least two-thirds of crown, with the amount of Orange Chrome tipping increasing posteriorly. Deep black feathers of the nape tipped with a circular dot of pure white. Lateral feathers of crown tipped with smaller dots of white, with a concentration of white dots above the eye, forming a small supraocular stripe. Entire back, rump and shoulders Yellowish Olive. Each feather double barred with Olive Yellow, imparting a pattern of faint barring to the dorsum. Primaries, secondaries and tertials Fuscous Brown with outer edge of secondaries and coverts Olive Yellow. Chin and throat dull white. Feathers of breast gray, barred and tipped with Straw Yellow. Proximal halves of abdominal feathers gray with distal halves heavily washed with Straw Yellow. Upper tail coverts barred like the back; undertail coverts Straw Yellow like the abdomen; tail black with middle pair of rectrices clear white on inner webs; underwing coverts and axillaries Straw Yellow. Wing, 50.0 mm; tail, 26.5 mm; culmen, 13.0 mm.

*Measurements*: Total of 12 specimens, including holotype. Adult males (7), wing 50.0-55.0 mm (average 51.9 mm); tail 25.0-29.0 mm (average 26.7 mm); culmen 12.0-14.5 mm (average 13.0 mm). Adult females (1), wing 52.0 mm; tail 27.0 mm; culmen 12.5 mm. Immatures (3 ♀♀, 1 ?), wing 50.0-

[1]Senior Curator of Ornithology, Los Angeles County Museum of Natural History.

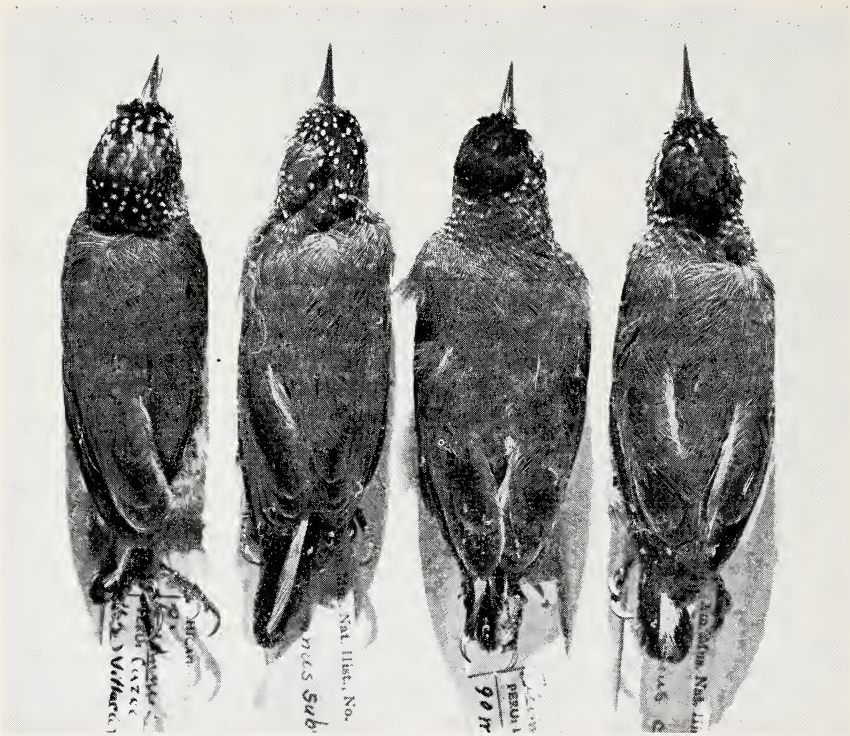

Figure 1. Dorsal view of *Picumnus subtilis* sp. nov. and *Picumnus castelnau*. From left to right, ♂ *P. subtilis* (type), ♀ *P. subtilis*, ♀ *P. castelnau*, and ♂ *P. castelnau*.

54.0 mm (average 51.6 mm); tail 24.0-27.0 mm (average 25.9 mm); culmen 12.0 mm.

*Range*: Known from a total of 12 specimens from the tropical foothills (Yungas) of east central Peru (Santa Rosa, upper Rio Ucayali, Dept. of Loreto, 200 m elev.) to southeastern Peru (Hacienda Villacarmen and Hacienda Cadena, Dept. of Cuzco, 1000 m elev. and Candamo, Dept. of Puno, 302 m elev.).

*Remarks*: Since the collection of the first specimen of this new piculet by H. Watkins at Candamo, Dept. of Puno, Peru, in 1916, its identity has remained obscure because of the tendency of workers to assign it to the species *Picumnus castelnau*, which it superficially resembles. The spotting of the crown and the barring of the chest of *P. subtilis*, however, immediately distinguish it from the latter (see Figs. 1 and 2). Despite the superficial resemblance to *P. castelnau* mentioned above, it is believed that this new piculet shows a definite affinity for the spot-crowned piculets rather than the immaculate

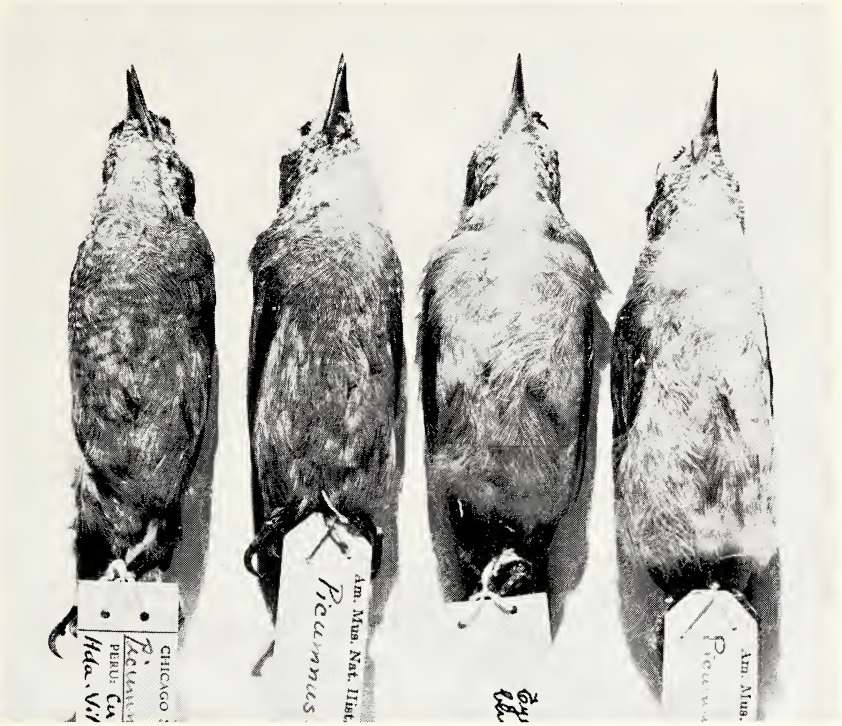


Figure 2. Ventral view of *Picumnus subtilis* sp. nov. and *Picumnus castelnau*. From left to right, ♂ *P. subtilis* (type), ♀ *P. subtilis*, ♀ *P. castelnau*, and ♀ *P. castelnau*.

crowned group consisting of *P. castelnau* and *P. fuscus*. At present *P. subtilis* and *P. castelnau* are known to be sympatric only in the area of the upper Rio Ucayali near its confluence with the Rio Urubamba. In the area of its greatest known abundance, in southeastern Peru, *P. subtilis* shares an area of sympatry with *Picumnus aurifrons*.

The type locality, Hacienda Villacarmen (12° 51′ S, 71° 15′ W), is described by E. R. Blake as "—lying just within the Dept. of Cuzco, being separated from the Dept. of Madre de Dios by the Rio Piña Piña, a minor tributary of the Rio Alto Madre de Dios—on the road from Cuzco to Manu." (pers. comm.)

The subtle yet distinct differences between *Picumnus castelnau* and this new piculet make the specific name *subtilis* seem appropriate.

*Specimens Examined*: (Holotype and 11 paratypes) American Museum of Natural History (AMNH), 6 (2 ♂♂, 1 ♀, 3 imm.), Santa Rosa, upper Rio Ucayali, Department of Loreto, Peru; Candamo, Department of Puno, Peru.

Field Museum of Natural History (FMNH), 2 ♂♂, Hacienda Villacarmen, Department of Cuzco, Peru (holotype) and Hacienda Cadena, Department of Cuzco, Peru. Peabody Museum of Yale University (PMYU), 4 ( 3♂♂, 1 ♀ imm.), Hacienda Cadena, Department of Cuzco, Peru.

For the loan of comparative material of *Picumnus subtilis* and *Picumnus castelnau*, I am indebted to the American Museum of Natural History, the Carnegie Museum, the Field Museum of Natural History, the Louisiana State University Museum of Zoology, and the Peabody Museum of Yale University.

This study has been supported in part by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History.

## SUMMARIO

En un estudio de revision de los pequeños Pájaros Carpinteros del genero *Picumnus* de Centro y Sur America se encontró una especies nó descrita en especimens de la región sur-este del Perú.

Esta nueva especie ha sido nombrada *Picumnus subtilis,* y es superficialmente parecida a *Picumnus castelnau*, aunque no están cercanamente relacionadas. El macho y la hembra de *P. castelnau* presentan crestas sin manchas, mientras que tanto el macho como la hembra de *P. subtilis* tienen manchas blancas en la cresta. *P. subtilis* fue identificada estudiando 12 especimens, encluyendo el holotipo.

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# A NEW SPECIES OF *EURHOPALOTHRIX* FROM EL SALVADOR (HYMENOPTERA: FORMICIDAE)

*By* ROY R. SNELLING

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DOROTHY M. HALMOS
*Editor*

# A NEW SPECIES OF *EURHOPALOTHRIX* FROM EL SALVADOR (HYMENOPTERA: FORMICIDAE)

*By* Roy R. Snelling[1]

Abstract: A new species of basicerotine ant is described from two worker specimens from El Salvador, Central America. This new species, placed in the genus *Eurhopalothrix*, is a member of the *E. bolaui* group and is most closely related to *E. speciosa*. It differs from this and other species in the number and arrangement of specialized hairs on the head and body.

Several years ago I was given a number of miscellaneous ants by Dr. R. O. Schuster, University of California, Davis. A single vial of Berlese sample material from El Salvador yielded six basicerotine ants; two specimens each of *Octostruma balzani* (Emery), a new species of *Eurhopalothrix* described below, and a new genus and species. The latter has been described by Brown and Kempf (1968).

Dr. Brown first recognized the following species as new and returned it to me for description, along with specimens of *E. speciosa* Brown and Kempf for comparison. I wish to thank both Dr. Brown and Dr. Schuster for their assistance.

## **Eurhopalothrix apharogonia** new species

Fig. 1

*Diagnosis*: A new species of the *E. bolaui* group as defined by Brown and Kempf (1960). It may be distinguished from other members of the group by the following combination of characters: four erect specialized hairs present on cephalic dorsum, no clavate hairs on posterior occipital angles, no erect clavate hairs on pronotal dorsum and posterior part of mesoscutum.

The abbreviations used in the following description are those of Brown and Kempf (1960).

*Holotype worker*: TL, 3.87; H1, 0.93; HW, 0.84 (CI, 90); scape L, 0.53; maximum diameter of compound eye, 0.03; WL, 1.12 mm. Form of head and body as shown in figures.

Appressed and subappressed ground pilosity similar to *E. speciosa, i.e.*, consisting largely of simple hairs, which are rather dense on mandibles and clypeus, sparse on petiolar nodes and gastric dorsum, very sparse and inconspicuous on vertex, occiput and thoracic dorsum; simple appressed hairs of tibiae replaced largely by appressed and decumbent spatulate or broadened hairs; larger specialized hairs thick-squamiform, smaller than corresponding hairs in *E. speciosa*; reduced in number on head, consisting of four rectangularly arranged hairs medially on occiput. Humeral pair absent in both speci-

[1]Entomology Section, Los Angeles County Museum of Natural History.

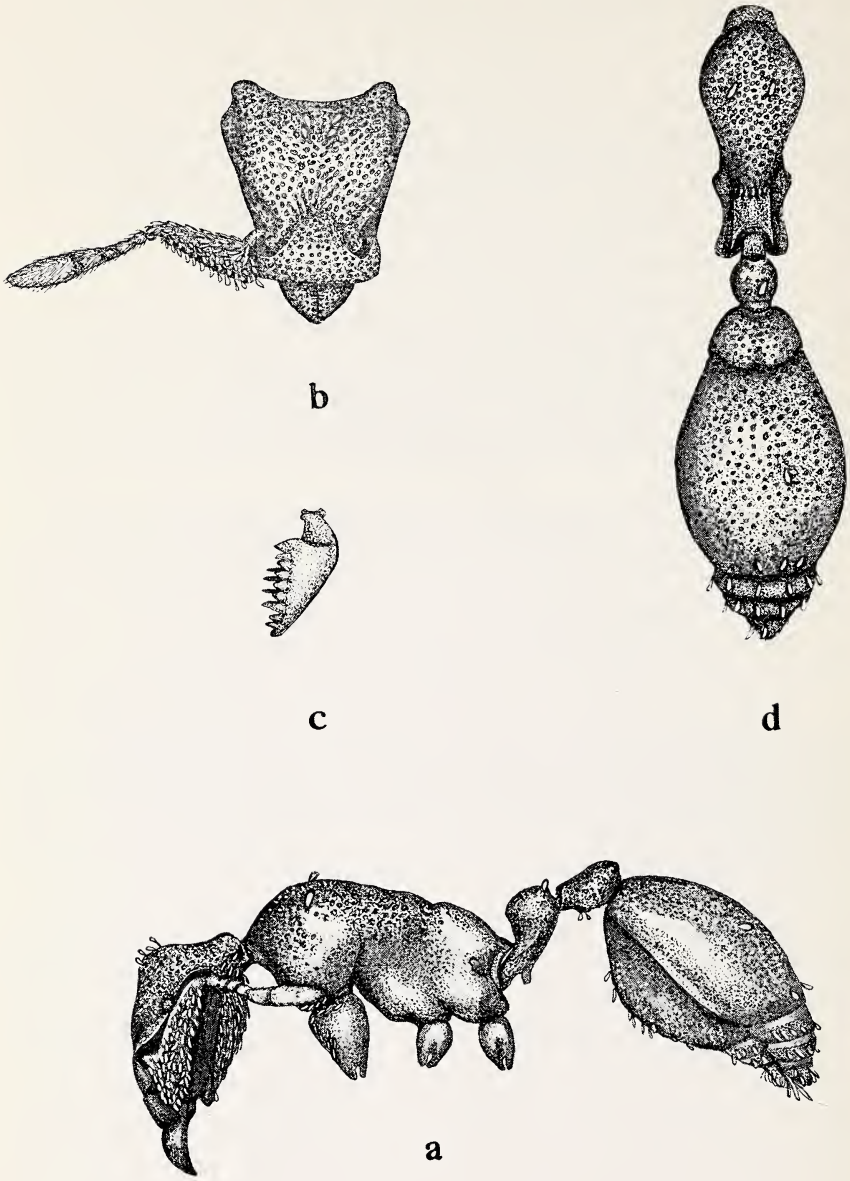


Figure 1. *Eurhopalothrix apharogonia*, new species. a, lateral aspect; b, frontal aspect of head; c, right mandible, enlarged; d, dorsal aspect of alitrunk and gaster. Illustrations by Ruth Ann DeNicola.

mens, presumably a real condition; a single pair present near middle of mesonotum, posterior pair lacking; postpetiole without dorsal clavate hairs. Median hairs lacking on first gastric segment of holotype (paratype has one median clavate hair; presumably one has been rubbed off).

Promesonotal suture obsolete; metanotal groove present but very poorly defined. Body somewhat shiny between moderate, rather close punctures; gastric pubescence sparser than that of thoracic dorsum; cephalic punctures denser on cephalic dorsum; finer on clypeus and distinctly separated. Mandibles shiny, finely punctate; masticatory margin with thirteen teeth, an outer set of ten, and an upper, inner set of three longer, spikelike teeth (Fig. 1). Color medium ferruginous, legs and antennae more yellowish.

*Holotype*: University of California, Davis, worker, EL SALVADOR, 4 miles north of Quetzaltepec, 7 July 1961, collected by M. E. Irwin.

*Paratype*: Worker, with same data as holotype, Los Angeles County Museum of Natural History.

Although *E. apharogonia* is one of the larger members of the *E. bolaui* group, it agrees with the smaller, more specialized species in the reduction of its erect pilosity. It is especially close to *E. speciosa* and *E. floridana* Brown and Kempf. From both of these it may be separated by the characters given in the key below, which is a modification of the appropriate portion of the key of Brown and Kempf (1960). The apical margins of the gastric segments are devoid of erect clavate hairs in the two specimens available to me. However, since these are consistently present in all other species of the group, as a group character, it seems logical that they are normally present in *E. apharogonia* also.

7. Dorsum of head with a single pair of erect clavate hairs on vertex, three pairs of erect clavate hairs on alitrunk, including one pair on pronotum (S Florida) ..... *floridana* Brown and Kempf

   Dorsum of head with two or three pairs of erect clavate hairs; one or two pairs of erect clavate hairs on alitrunk, none present on pronotum ..... 8

8. Dorsum of head with three pairs of erect clavate hairs, one on each posterior occipital corner and two pairs arranged in a close rectangle on vertex; mesonotum with two pairs of erect clavate hairs (SE Brazil) ..... *speciosa* Brown and Kempf

   Dorsum of head with two pairs of erect clavate hairs, arranged in a close rectangle on vertex; mesonotum with a single pair of erect clavate hairs (El Salvador) ..... *apharogonia* Snelling

The name of this new taxon is derived from the Greek *aphares*, unclad, and *gonia*, angle or corner, in allusion to the lack of clavate hairs on the posterior occipital angles.

## RESUMEN

Una nueva especie de hormiga basicerotina, *Eurhopalothrix apharogonia,* es descrita como nueva especie basado en el estudio de dós ejemplares de hormigas obreras. Estas hormigas fuéron obtenidas cuatro millas al Norte de Quetzaltepec, El Salvador, America Central. Esta nueva especie há sido colocada en el genero *Eurhopalothrix.* Es un miembro del grupo *E. bolaui* y está estrechamente relacionada con *E. speciosa.* Esta difiere de todas otras especies del grupo *E. bolaui* en la combinación de caracteres que sigue: cuatro pélos especializados y eréctos en el dórsum cefálico, ausencia de pelos en forma el remo en los ángulos occipitales posteriores y ausencia de pélos eréctos en forma de remo en la región pronotal dorsal y la parte posterior del mesoscutum.


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